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WOOD ANATOMY OF THE NEW WORLD PITHECELLOBIUM (SENSU LATO)[1]

DANIEL L. CASSENS AND REGIS B. MILLER

THE NEW WORLD *Pithecellobium* Martius s.l. consists of over 150 species of shrub- to tree-size plants. These species are mostly plants of tropical areas, ranging throughout Central and South America and the West Indies. In addition, *Ebenopsis* Britton & Rose and some species of *Havardia* Small occur in Texas and Mexico, and the range of a few species of *Pithecellobium* sensu stricto extends into southern Florida. The habitat of *Pithecellobium* s.l. is generally dry to mesic, but some species of *Zygia* P. Browne grow in or near water. Few specific uses of the wood are reported. However, some species of *Abarema* Pittier, *Arthrosamanea* Britton & Killip, *Cojoba* Britton & Rose, *Marmaroxylon* Killip, and *Samanea* Merr. reach tree size and are used locally. Occasionally these woods appear in foreign markets, where they may have commercial potential.

Pithecellobium s.l. is a mimosoid legume in the tribe Ingeae, which is characterized by Mohlenbrock (1963a) as follows: Calyx and corolla generally 5-lobed, cupular or tubular. Stamens numerous, indefinite, connate for a portion of their length. Ovary generally unicarpellate, but carpels varying from 1 to 15 per flower. Leaves usually bipinnate, once-pinnate in a few species; glands frequently present along winged or unwinged rachis; stipular spines sometimes present. Fruit or legume flat, terete, or moniliform; coriaceous, ligneous, fleshy, or papery; dehiscent, elastically dehiscent, or indehiscent and breaking irregularly and transversely between the seeds.

In 1874 Bentham recognized that the legume of *Pithecellobium* s.l. was diverse and described it as compressed; coriaceous, hard, or subfleshy; arcuate, circinnate, or rarely suberect; and indehiscent or dehiscent. The valves after

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dehiscence are often twisted, but not elastic. Bentham relied heavily on this diversity of the legume to characterize his sections and series. Later taxonomists used the manner of legume dehiscence, the presence or absence of spines and arils, and leaf characters to distinguish segregate genera of *Pithecellobium* s.l.

The splitting of the New World *Pithecellobium* s.l. began with the formation of *Havardia* and *Siderocarpos* by Small (1901). Merrill (1916) described *Samanea*, Fawcett and Rendle (1920) revived *Zygia*, and Pittier (1927) described *Abarema*. Britton and Rose (1928) described *Chloroleucon*, *Cojoba*, *Ebenopsis* (= *Siderocarpos*), *Jupunba*, *Painteria*, and *Punjuba* as new genera and also recognized *Havardia*, *Samanea*, and *Zygia*. *Pseudosamanea* was described by Harms (1930), and later Britton and Killip (1936) described *Klugiodendron* and *Arthrosamanea*. In the same publication Britton and Rose founded *Macrosamanea*. Finally, Killip described *Marmaroxylon* (Record, 1940).

More recent taxonomic publications (Burkart, 1949; Dugand, 1948, 1966; Hutchinson, 1964; Kleinhoonte, 1940; Mohlenbrock, 1963a, 1963b) continue to recognize at least some segregates of *Pithecellobium*. Other publications (Irwin, 1966; Macbride, 1943; Cowan, 1961; Standley & Record, 1936; Standley & Steyermark, 1946; Woodson & Schery, 1950), however, indicate that *Pithecellobium* should not be divided into segregate genera.

Kostermans (1954) completed a monograph of the Asiatic, Malaysian, Australian, and Pacific species of Mimosaceae formerly included in *Pithecellobium*. Newly described genera include *Morolobium* Kosterm. (one species), *Parasamanea* Kosterm. (one species), *Serialbizzia* Kosterm. (two species), *Parenterolobium* Kosterm. (one species), *Cylindrokelupka* Kosterm. (three species), and *Paralbizzia* Kosterm. (three species). Kostermans reinstated *Cathormion* Hassk. (one species) and recognized *Zygia* (four species), *Painteria* (one species), and *Abarema* (44 species).

Maintaining *Pithecellobium* as one large genus or reducing it to several smaller ones continues to be the basis for considerable disagreement among taxonomists. Therefore, it was concluded that an investigation of the secondary xylem might provide additional information for developing a more acceptable classification system. Classical diagnostic features of the secondary xylem were examined to determine whether certain species form distinct groups. Observations of the secondary xylem can help determine the validity of a genus, and in complicated situations it can provide evidence for supporting or negating morphological findings. Thus, each of the groups recognized was compared with the proposed generic segregates. It was reasoned that if the groups and the generic segregates correspond, the secondary xylem provided evidence for the formation of distinct taxa within the *Pithecellobium* complex. However, if the secondary xylem is homogeneous, or the groups and the generic segregates do not correspond, the evidence would suggest maintaining *Pithecellobium* in a broad sense.

In addition, the relationships and specialization levels of different tissues are described and discussed. A practical benefit derived from an investigation of the secondary xylem is based on the macroscopic and microscopic characters that are key aids in the identification of unknown wood specimens.

MATERIALS AND METHODS

TABLE 1 lists the 266 wood specimens of 83 species examined from the *Pithecellobium* complex. All of the wood specimens included here have herbarium vouchers. Additional specimens and species without vouchers are included by Cassens (1973).

In all cases this investigation is based on the secondary xylem; hence, the use of such terms as "*Abarema* wood-type." The name *Abarema* may also be used in another sense; that is, as a particular genus segregated from *Pithecellobium*. The placement of a species with a different generic name into a particular wood type does not imply a taxonomic transfer of the epithet into that segregate genus. However, it does indicate the anatomical similarities of all species included in that wood type.

Standard methods were used in the preparation and examination of all microscope slides. However, some measurements need further explanation. For example, length measurements were taken for 25 vessel elements and 25 fibers. An average pore diameter was obtained by measuring 25 of the larger pores and then averaging the 10 largest. A numerical distribution of pores was determined from counts in 10 fields that covered a total of 8.48 sq. mm.

Ray width and height were calculated by cell count and micrometer measurements. Widths in micrometers were obtained from the measurement of 10 rays at their widest point. If the rays were less than 20 cells high, the height in micrometers and number of cells was calculated by measuring 25 of the higher rays and then averaging the 10 highest. Rays higher than 20 cells were only measured in micrometers.

For the wood descriptions, an average of all the specimens was calculated. For example, if the grand average was 900 and the lowest and highest specimen averages were 800 and 1000, respectively, then the figures are reported in the anatomical descriptions in the form "800(–900)–1000." The standard size classes for pore diameter and distribution, vessel element and fiber length, and intervascular pits are reported according to the definitions of the Committee on the Standardization of Terms of Cell Size (1937, 1939), Chattaway (1932), and Record and Chattaway (1939).

For each specimen the occurrence of amorphous inclusions, crystals, and natural saponins is reported. The crystal type, shape, and arrangement within the particular cell type was observed. When crystals were surrounded by a sheath that did not disintegrate when treated with Jeffrey's maceration solution or hydrofluoric acid, they are termed "integumented."

To test for the presence or absence of natural saponins, small chips of heartwood were placed in a vial and covered with distilled water. The vial was shaken by hand for several seconds. If very little or no froth appeared, the test was considered negative. If froth appeared and then disappeared in a few seconds, the test was "short positive." If abundant froth appeared and remained, the test was positive.

The fluorescence of dry heartwood is a character used for identification purposes. A freshly exposed wood surface was placed under a long-wave

TABLE 1. **Wood specimens examined for each wood type.**

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	ABAREMA WOOD-TYPE			
Jupunba abbottii (Rose & Leonard) Britton & Rose				
	Anonymous s.n.	Dominican Republic	US	MADw 19522
Pithecellobium arenarium Ducke				
	Maguire 42959	Guyana	NY	MADw 25501
Pithecellobium auriculatum Bentham				
	Krukoff 7938	Brazil	US	MADw 25412
Samanea corymbosa (Rich.) Pittier				
	Krukoff 6743	Brazil	US	SJRw 36856
	Stahel 360	Surinam	MAD	SJRw 42664
	FDBG 2498	Guyana	K	SJRw 43630
	Ducke 396	Brazil	MAD	SJRw 44314
	Anonymous (WIBw 1047)	Surinam	U?	SJRw 49773
Pithecellobium elegans Ducke				
	Navy Project 136, F12	Brazil	MAD	SJRw 45543
	FDBG 4805	Guyana	K	SJRw 46466
Pithecellobium fanshawei Sandwith				
	FDBG 4181 (type)	Guyana	NY	SJRw 46467

Pithecellobium gonggrijpii Kleinhoonte			
Lanjouw & Lindeman 518	Surinam	U	MADw 25489
Stahel 88	Surinam	MAD	SJRw 41157
FDBG 3313	Guyana	K	SJRw 43744
Maguire 24273	Surinam	NY	SJRw 44106
Abarema jupunba (Willd.) Britton & Killip			
Maguire 51953	Brazil	NY	MADw 21611
Ll. Williams 12047	Venezuela	F	MADw 25413
Persaud 64	Guyana	F	SJRw 9472
Capucho 593	Brazil	F	SJRw 23887
McArthur s.n.	Surinam	MAD	SJRw 32241
Stahel 20	Surinam	US	SJRw 42432
FDBG 3255	Guyana	K	SJRw 43730
Beard 8	Grenada	A	SJRw 49510
Maguire 40552	Guyana	NY	SJRw 50123
Inst. Nat. Sci. 17670	Colombia	COL	SJRw 52872
Pithecellobium langsdorfii Bentham			
Whitford 351	Brazil	MAD	SJRw 3174
Hoehne 29842	Brazil	MAD	SJRw 23833
Reitz & Klein 3912	Brazil	MAD	SJRw 52072
Samanea leucocalyx Britton & Rose			
McClay & Clara 41	Guatemala	MAD	MADw 23152
Brown II	Belize	MAD	SJRw 13021
Pithecellobium leucophyllum Spruce ex Bentham			
Wurdack & Adderley 43317	Venezuela	NY	SJRw 54393

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	ABAREMA WOOD-TYPE, continued			
Samanea macradenia (Pittier) Britton & Rose				
	Christopherson 196 (type)	Panama	US	MADw 5718
	USNH 716482	Panama	US	SJRw 53764
Samanea marginata (Spruce ex Bentham) Pittier				
	Krukoff 6715	Brazil	US	SJRw 36841
	Ll. Williams 14869	Venezuela	F	SJRw 41806
Pithecellobium mataybifolium Sandwith				
	Cowan 39332	Guyana	NY	SJRw 50101
Jupunba obovalis (A. Rich.) Britton & Rose				
	Alberto J. Fors 106	Cuba	SV?	MADw 14418
Pithecellobium panurense Spruce ex Bentham				
	Wurdack & Adderley 54364	Venezuela	NY	SJRw 54364
Samanea pedicellaris (DC.) Killip				
	Maguire et al. 51777	Brazil	NY	MADw 21470
	Gutierrez R.85, R.111	Peru	MAD	MADw 22364
	FDBG s.n.	Guyana	K?	SJRw 32845
	Krukoff 10886	Bolivia	MAD	SJRw 39720

Ducke 354	Brazil	MAD	SJRw 40085
Stahel 125	Surinam	MAD	SJRw 41190
Stahel 237	Surinam	MAD	SJRw 42466
FDBG 3201	Guyana	K	SJRw 43611
Anonymous (WIBw 1059)	Surinam	U?	SJRw 49778
Jupunba pinetorum (Britton) Britton & Rose			
Bucher 11	Cuba	MAD	SJRw 14728
Jupunba pseudo-tamarindus Britton			
Cooper 461 (type)	Panama	MAD	SJRw 12079
Pithecellobium villiferum Ducke			
Maguire 24629	Surinam	NY	SJRw 44177
Wurdack & Adderley 43351	Venezuela	NY	SJRw 54373

ALBIZIA WOOD-TYPE

Albizia adinocephala (Donn. Smith) Britton & Rose			
Dayton 3097	Costa Rica	MAD	MADw 10300
Record & Kuylen H.20	Honduras	MAD	SJRw 9966
Albizia caribaea (Urban) Britton & Rose			
Holdridge 6281	Panama	MO	MADw 24821
Ll. Williams 9720	Mexico	F	SJRw 34966
Curran & Turner V129	Venezuela	MAD	SJRw 45652
Turner V136	Venezuela	MAD	SJRw 45680
Curran & Turner V148	Venezuela	MAD	SJRw 45706
Albizia colombiana Britton			
Record & Kuylen 75 (type)	Colombia	MAD	SJRw 16474
Dugand 45	Colombia	MAD	SJRw 22478
Dugand 487	Colombia	MAD	SJRw 23920

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	ALBIZIA WOOD-TYPE, continued			
Pithecellobium glabripetalum H. S. Irwin	FDBG 5397 (type) (distributed as Pithecellobium niopoides Bentham)	Guyana	K	SJRw 46468
Albizia hassleri (Chodat) Burkart	Woolston T10	Paraguay	MAD	SJRw 48286
Albizia tomentosa (M. Micheli) Standley	Record B.H.27 (type)	Belize	MAD	SJRw 8795
	Brown 5	Belize	MAD	SJRw 13024
	Ll. Williams 8771	Mexico	F	SJRw 34689
	Ll. Williams 9863	Mexico	MAD	SJRw 34820
	ARTHROSAMANEA WOOD-TYPE			
Arthrosamanea multiflora (H.B.K.) Kleinhoonte	Novenaz 37	Argentina	MAD	SJRw 14993
	Capucho 451	Brazil	F	SJRw 22742
	Krukoff 6750	Brazil	US	SJRw 36861
Arthrosamanea pistaciaefolia (Willd.) Britton & Rose	Ll. Williams 12823	Venezuela	F	MADw 25493

Curran 43	Colombia	MAD	SJRw 1551
Curran 44	Colombia	MAD	SJRw 1552
Curran 300	Colombia	MAD	SJRw 1528
Dugand 138, 483	Colombia	MAD	SJRw 23915
Dugand 296	Colombia	F	SJRw 28504

CHLOROLEUCON WOOD-TYPE

Pithecellobium acacioides Ducke			
Capucho 356	Brazil	F	SJRw 21659
Chloroleucon guantanamense (Britton) Britton & Rose			
Bucher 81	Cuba	MAD	SJRw 16252
Chloroleucon leucospermum (Brandegee) Britton & Rose			
Winzerling II-2	Belize	MAD	SJRw 9851
Record & Kuylen H.59	Honduras	MAD	SJRw 10005
Chloroleucon mangense (Jacq.) Britton & Rose			
Dugand 220, 57	Colombia	MAD	SJRw 22509
Dugand 315, 150	Colombia	MAD	SJRw 23927A
Navy Project 433	Panama	MAD	SJRw 45673
Navy Project 452	Panama	MAD	SJRw 45677
Navy Project 453	Panama	MAD	SJRw 45678
Navy Project 454	Panama	MAD	SJRw 45679
Stern & Chambers 158	Panama	MAD	SJRw 51650
Pithecellobium mathewsii Bentham			
Ll. Williams 5532	Peru	F	MADw 15936
Ll. Williams 5967	Peru	F	MADw 15937
Ll. Williams 6463	Peru	F	MADw 15938

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	CHLOROLEUCON WOOD-TYPE, continued			
Chloroleucon tortum (Martius) Pittier				
	Alberto J. Fors 27	Cuba	SV?	MADw 15860
	Ll. Williams 12879	Venezuela	F	MADw 25494
	Curran 331	Brazil	MAD	SJRw 1943
	Pittier 12363	Venezuela	MAD	SJRw 10345
Chloroleucon vinhatico (Record) Record				
	Curran 59 (type)	Brazil	MAD	SJRw 1806
	Curran 28	Brazil	F	SJRw 4698
Chloroleucon sp.				
	Curran & Haman 562	Venezuela	GH	SJRw 2832
	Curran 737	Venezuela	GH?	SJRw 16181
	COJOBA WOOD-TYPE			
Cojoba arborea (L.) Britton & Rose				
	Alberto J. Fors 953	Cuba	SV?	MADw 13967
	Ll. Williams 9465	Mexico	F	MADw 15935
	Anonymous s.n.	Jamaica	US	MADw 20724
	Britton & Kramer XV	Puerto Rico	MAD	SJRw 3088
	Whitford & Stadtmiller 9A	Honduras	MAD	SJRw 3676

Hope II	Belize	MAD	SJRw 4797
Record 19	Belize	MAD	SJRw 8787
Gill & Whitford 50	Cuba	MAD	SJRw 9061
Gill & Whitford 124	Cuba	MAD	SJRw 9135
Mathews & Crosby 67	Cuba	MAD	SJRw 9220
Stevenson & Burns II	Belize	F	SJRw 9564
Brown III	Belize	MAD	SJRw 13022
Yuncker et al. 6157	Honduras	MAD	SJRw 33748
Ll. Williams 8805	Mexico	MAD	SJRw 34700
Stevenson 230	Belize	MAD	SJRw 37258
Shank 92	Nicaragua	MAD	SJRw 46882
Cojoba costaricensis Britton & Rose			
Austin Smith s.n.	Costa Rica	MAD	SJRw 38353
Cojoba donnell-smithii Britton & Rose			
Record G.138	Guatemala	MAD	SJRw 10089
Stevenson III	Belize	MAD	SJRw 14893
Pithecellobium membranaceum (Bentham) Schery			
Stern et al. 1131	Panama	US	SJRw 55040
Cojoba rufescens (Bentham) Britton & Rose			
Roadmaster Panama RR 40	Panama	MAD	SJRw 7239
Dugand 604	Colombia	MAD	SJRw 27126
Stern et al. 45	Panama	US	SJRw 54590
Cojoba sophorocarpa (Bentham) Britton & Rose			
Stevenson 6	Belize	MAD	SJRw 10688
Galusser 20	Guatemala	MAD	SJRw 10740

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	COJOBA WOOD-TYPE, continued			
Cojoba tenella Britton & Rose	Hottle 54	Honduras	F	SJRw 15631
	EBENOPSIS WOOD-TYPE			
Ebenopsis flexicaulis (Bentham) Britton & Rose	Nogle 99	Texas	TAES	MADw 13215
	Wilson M-1	Mexico	MAD	MADw 18344
	MEXFw X-324	Mexico	ICF	MADw 25290
	HAVARDIA WOOD-TYPE			
Havardia leiocalyx (Standley) Britton & Rose	Page 9615	Mexico	DS	MADw 23863
Havardia pallens (Bentham) Britton & Rose	Wilson M-7	Mexico	MAD	MADw 18342
	Scott s.n.	Miami, Florida†	?	SJRw 44776
	Cavazos 62A	Mexico	US	USw 19246
Havardia platyloba (Sprengel) Britton & Rose	Curran & Haman 400	Curaçao	GH	SJRw 2775

Record & Don Jaca 51	Colombia	MAD	SJRw 16450
Dugand 1158	Colombia	MAD	SJRw 35287

KLUGIODENDRON WOOD-TYPE

Klugiodendron laetum (Poeppig & Endl.) Britton & Killip

Ll. Williams 4190	Peru	F	MADw 15942
Krukoff 6457	Brazil	US	SJRw 36693
King 6170	Colombia	US	USw 37504

MACROSAMANEA WOOD-TYPE

Macrosamanea aquatica Pittier

Wurdack & Adderley 42732	Venezuela	NY	SJRw 54144

Pithecellobium consanguineum Cowan

Maguire et al. 41878 (type)	Guyana	NY	MADw 25503

Macrosamanea discolor (Humb. & Bonpl.) Britton & Rose

NYBG 28422	Guyana	NY	MADw 25502

Macrosamanea kegelii (Meissner) Kleinhoonte

Gonggrijp 4150	Surinam	NY	MADw 25682

Macrosamanea simabifolia (Spruce ex Bentham) Pittier

Wurdack & Adderley 43023	Venezuela	NY	SJRw 54466
Wurdack & Adderley 42937	Venezuela	NY	SJRw 54521

MARMAROXYLON WOOD-TYPE

Pithecellobium basijugum Ducke

Lanjouw & Lindeman 2270	Surinam	U	MADw 25486
Wurdack & Maguire 41958	Guyana	NY	MADw 25504

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	MARMAROXYLON WOOD-TYPE, continued			
Pithecellobium collinum Sandwith				
	FDBG 3976 (type)	Guyana	K	SJRw 46465
Pithecellobium dinizii Ducke				
	Krukoff 1302	Brazil	US	MADw 25118
	Cuatrecasas 17374	Colombia	F	SJRw 43205
Marmaroxylon racemosum (Ducke) Killip				
	BAFOG 81M	French Guiana	U	MADw 25487
	Van Hall 63	Surinam	U	MADw 25488
	Dahlgren s.n.	Brazil	F	SJRw 16780
	Ducke 39†	Brazil	MAD	SJRw 20720
	Capucho 274	Brazil	F	SJRw 21260
	Capucho 377	Brazil	F	SJRw 22055
	Smith 2721	Guyana	MAD	SJRw 35676§
	Stahel 72	Surinam	MAD	SJRw 41145
	FDBG 3114	Guyana	K	SJRw 46469
Pithecellobium umbriflorum Ducke				
	Krukoff 6872	Brazil	F	SJRw 36937

PITHECELLOBIUM (SENSU STRICTO) WOOD-TYPE

Pithecellobium dulce (Roxb.) Bentham			
Mell s.n.	Florida	US?	MADw 5122
Acosta-Solís 11930	Ecuador	F	MADw 11155
Alberto J. Fors 242	Cuba	SV	MADw 13887
Curran & Haman 502	Venezuela	GH	SJRw 2816
Pittier 11760	Venezuela	MAD	SJRw 7746
Record & Kuylen G.107	Guatemala	MAD	SJRw 10058
Record 32	Colombia	MAD	SJRw 16431
Record 43	Colombia	MAD	SJRw 16442
Record 59	Colombia	MAD	SJRw 16458
Espina & Giacometto B8A	Colombia	MAD	SJRw 20990
Dugand 223, 60	Colombia	MAD	SJRw 22512
Dugand 574	Colombia	MAD	SJRw 27104
Ll. Williams 9760	Mexico	F	SJRw 34984
Caldwell 8755	Florida	MAD	SJRw 49282
Pithecellobium guadalupense (Pers.) Chapman			
Stern 131	Florida Keys	MAD	SJRw 49457
Stern & Brizicky 193	Florida Keys	MAD	SJRw 51043
Stern & Brizicky 205	Florida Keys	MAD	SJRw 51054
Stern & Brizicky 358	Florida Keys	MAD	SJRw 51174
Stern & Brizicky 362	Florida Keys	MAD	SJRw 51178
Stern & Chambers 252	Florida Keys	MAD	SJRw 51464
Pithecellobium lanceolatum (Humb. & Bonpl.) Bentham			
Ll. Williams 12888	Venezuela	F	MADw 25152
Mell 19	Mexico	MAD	SJRw 6997
Record & Kuylen 39	Colombia	MAD	SJRw 16438
Pithecellobium microchlamys Pittier			
Dugand 345, 777	Colombia	MAD	SJRw 29622

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	PITHECELLOBIUM (SENSU STRICTO) WOOD-TYPE, continued			
Pithecellobium oblongum Bentham				
	Record & Kuylen G.120	Guatemala	MAD	SJRw 10071
	Stern & Chambers 27	Panama	MAD	SJRw 51544
Pithecellobium oblongum Pittier				
	Dugand 847	Colombia	MAD	SJRw 29678
Pithecellobium unguis-cati (L.) Bentham				
	Wilson F-5	Florida	MAD	MADw 15950
	Curran & Haman s.n.	Curaçao	IGH	MADw 19474
	Anonymous s.n.	Florida	US	MADw 20978
	MacDonald 24	Florida	MAD	SJRw 32536
	MacDonald 49	Florida	MAD	SJRw 32561
	Caldwell	Florida	MAD	SJRw 49290
	Stern & Brizicky 257	Florida	MAD	SJRw 51096
	Stern et al. 448	Florida	MAD	SJRw 51232
Pithecellobium sp.				
	Curran 425	Curaçao	GH	SJRw 2798
	Curran 616	Curaçao	GH	SJRw 2854

PSEUDOSAMANEA WOOD-TYPE

Albizia cubana Britton & Wilson			
Brother H. Leon 13720	Cuba	F	SJRw 16321
Pseudosamanea guachapele (H.B.K.) Harms			
Humberto Tasayco Tasayco 3	Peru	MAD	MADw 22546
Acosta-Solís 13003	Ecuador	F	MADw 25414
Acosta-Solís 11964	Ecuador	F	MADw 25415
Pittier 12184	Venezuela	MAD	SJRw 9520
Record & Kuylen G.126	Guatemala	MAD	SJRw 10077
Dugand 540	Colombia	MAD	SJRw 27084
Dugand 560	Colombia	MAD	SJRw 27093
Acosta-Solís 11716	Ecuador	F	SJRw 45429
Navy Project 79	Honduras	MAD	SJRw 45518
Dunlap s.n.	Honduras	MAD	SJRw 45796
Forgeson 77B	Panama	MAD	SJRw 50973

PUNJUBA WOOD-TYPE

Punjuba racemiflora (Donn. Smith) Britton & Rose			
Barbour 1014	Costa Rica	MAD	MADw 10284

SAMANEA WOOD-TYPE

Samanea saman (Jacq.) Merrill			
Whitford & Stadtmiller s.n.	Guatemala-Honduras Boundary	US	MADw 10851
Sarlin G50	Haiti	P	MADw 16946
RPPRw Tree 54	Puerto Rico	RPPR	MADw 17491
Anonymous s.n.	Venezuela	MER	MADw 23994
Curran 302	Colombia	MAD	SJRw 1529

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	SAMANEA WOOD-TYPE, continued			
	Gill & Whitford 90	Cuba	MAD	SJRw 9101
	Cooper 442	Panama	MAD	SJRw 12060
	Ll. Williams 5495	Peru	F	SJRw 18758
	Espina & Giacometto A202	Colombia	MAD	SJRw 20977
	Capucho 479	Brazil	F	SJRw 22770
	Scarff 12G	Dominican Republic	MAD	SJRw 35404
	Smith 3316	Guyana	MAD	SJRw 35900
	Turner 111	Venezuela	MAD	SJRw 45751
	Turner 120	Venezuela	MAD	SJRw 45752
	Schmidt 99	Bolivia	HBG	SJRw 50188
Samanea saman (Jacq.) Merrill var. acutifolium Bentham				
	Woytkowski 35145	Colombia	MAD	SJRw 44592
	ZYGIA WOOD-TYPE			
Zygia ampla (Spruce ex Bentham) Pittier				
	Ll. Williams 14747	Venezuela	F	SJRw 41738
Zygia cauliflora (Willd.) Killip				
	Maguire 55773	Surinam	NY	MADw 22954
	Ll. Williams 11424	Venezuela	F	MADw 25120
	BAFOG 172M	French Guiana	U	MADw 25485

Persaud 99	Guyana	F	SJRw 9493
Persaud 106	Guyana	F	SJRw 9496
Smith 2588	Guyana	MAD	SJRw 35617
Stahel 284	Surinam	MAD	SJRw 42513
Zygia cognata (Schlecht) Britton & Rose			
Ll. Williams 9208	Mexico	MAD	SJRw 34792
Zygia conzattii (Standley) Britton & Rose			
Ll. Williams 9438	Mexico	F	SJRw 34857
Zygia divaricata (Brongniart) Pittier			
Ll. Williams 15027	Venezuela	F	SJRw 41895
Wurdack & Adderley 43419	Venezuela	NY	SJRw 54536
Zygia englesingii (Standley) Record			
Englesing 205 (type)	Nicaragua	MAD	SJRw 13297
Zygia glomerata (Vell.) Pittier			
Ll. Williams 14238	Venezuela	F	SJRw 41472
Wurdack & Adderley 43314	Venezuela	NY	SJRw 54516
Zygia inaequalis (Poiret) Pittier			
Espina & Giacometto A72	Colombia	MAD	SJRw 20847
Ducke 384	Brazil	MAD	SJRw 40412
Ll. Williams 15172	Venezuela	F	SJRw 41995
Ll. Williams 15460	Venezuela	F	SJRw 42128
Wurdack & Adderley 42674	Venezuela	NY	SJRw 54490
Pithecellobium juruanum Harms			
Krukoff 4746	Brazil	F	MADw 18544

TABLE 1. **Wood specimens examined for each wood type** (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
	ZYGIA WOOD-TYPE, continued			
Zygia latifolia (L.) Fawcett & Rendle				
	Krukoff 5798	Brazil	F	MADw 25119
	Persaud 63	Guyana	F	SJRw 9471
	Krukoff 6212	Brazil	F	SJRw 36517
	Cuatrecasas 14251	Colombia	US	SJRw 42739
	FDBG 3618	Guyana	K	SJRw 46562
Zygia longifolia (Humb. & Bonpl.) Britton & Rose				
	Gutierrez R.74, R.93	Peru	MAD	MADw 22402
	Stern et al. 1897	Panama	US	MADw 24320
	Kluge 23	Panama	MAD	SJRw 7136
	Cooper & Slater 54	Panama	MAD	SJRw 10152
	Record & Kuylen 14	Colombia	MAD	SJRw 16413
	Danforth 45	Costa Rica	MAD	SJRw 32968
Zygia peckii (Robinson) Britton & Rose				
	Winzerling s.n.	Belize	F	SJRw 10172

Zygia recordii Britton & Rose			
Whitford & Stadtmiller 64	Guatemala-Honduras Boundary	MAD	SJRw 3724
Record & Kuylen G.5 (type)	Guatemala	MAD	SJRw 8836
Winzerling I-20	Belize	MAD	SJRw 9869
Zygia stevensonii (Standley) Record			
Stevenson II (type)	Belize	MAD	SJRw 3338
Kinlock 17	Belize	MAD	SJRw 17141
Zygia cf. *unifoliolata* (Bentham) Pittier			
Krukoff 6710	Brazil	US	SJRw 36838
Krukoff 6716	Brazil	US	SJRw 36842
Zygia sp.			
Stevenson 90	Belize	F	SJRw 35021
Krukoff 10798	Bolivia	F	SJRw 39662

* Arranged alphabetically by specific epithet.
† From U. S. Plant Introduction Garden.
‡ Published incorrectly as *A. Ducke 30* in Trop. Woods 63: 2. 1940.
§ Published incorrectly as SJRw 35671 in *ibid.*

ultraviolet light to reveal the presence or absence of yellowish fluorescence.

The specific gravity of several representative specimens was determined by the water-displacement technique. Oven-dry weight and volume at 5 percent moisture content were used in all calculations. The specific gravity for each wood type is given along with its class as defined by Panshin and de Zeeuw (1970).

KEY TO WOOD TYPES

A. Parenchyma confluent, sometimes aliform.
  B. Septate fibers present.
    C. Rays bi- to quadriseriate. . . . . *Arthrosamanea.*
    C. Rays uniseriate (available specimens small). . . . *Macrosamanea.*
  B. Septate fibers absent.
    D. Heartwood light brown with dark bands or totally dark brown. . . . . *Marmaroxylon.*
    D. Heartwood light yellow without dark bands. . . . . *Zygia.*

A. Parenchyma vasicentric, sometimes aliform.
  E. Septate fibers present.
    F. Rays bi- to quadriseriate; heartwood light yellow, rarely light brown. . . . . *Albizia* or *Arthrosamanea.*
    F. Rays uniseriate; heartwood dark brown or red-brown.
      G. Heartwood dark brown. . . . . .*Havardia* (except *H. pallens*).
      G. Heartwood red-brown.
        H. Specific gravity 0.46–0.56. . . . . *Havardia pallens.*
        H. Specific gravity 0.63–1.00. . .*Pithecellobium* (sensu stricto).
  E. Septate fibers absent.
    I. Intervascular pit diameter 3–4 μm. . . . . *Cojoba.*
    I. Intervessel pit diameter 5–10 μm.
      J. Rays bi- or triseriate.
        K. Intervascular pit diameter 7–10 μm.; heartwood dark brown. . . . . *Samanea.*
        K. Intervascular pit diameter 6 μm.; heartwood yellow-brown. . . . . *Chloroleucon vinhatico.*
      J. Rays uniseriate or only partially biseriate (any one specimen may have a few biseriate rays).
        L. Diameter of largest pores averaging ca. 225 μm.; 3 or 4 pores or pore multiples/sq. mm.
          M. Intervascular pit diameter 6–8 μm.; fluorescence bright yellow. . . . . .*Pseudosamanea.*
          M. Intervascular pit diameter 5–6 μm.; fluorescence negative to yellow. . . . . *Abarema.*
        L. Diameter of largest vessels averaging ca. 130 μm.; 10 to 15 pores or pore multiples/sq. mm.
          N. Heartwood vessels completely occluded with dark, amorphous substance; heartwood dark brown; wood with oily feel. . . . . *Ebenopsis.*
          N. Heartwood vessels not completely occluded with dark, amorphous substance; heartwood yellow- or red-brown; wood without oily feel.

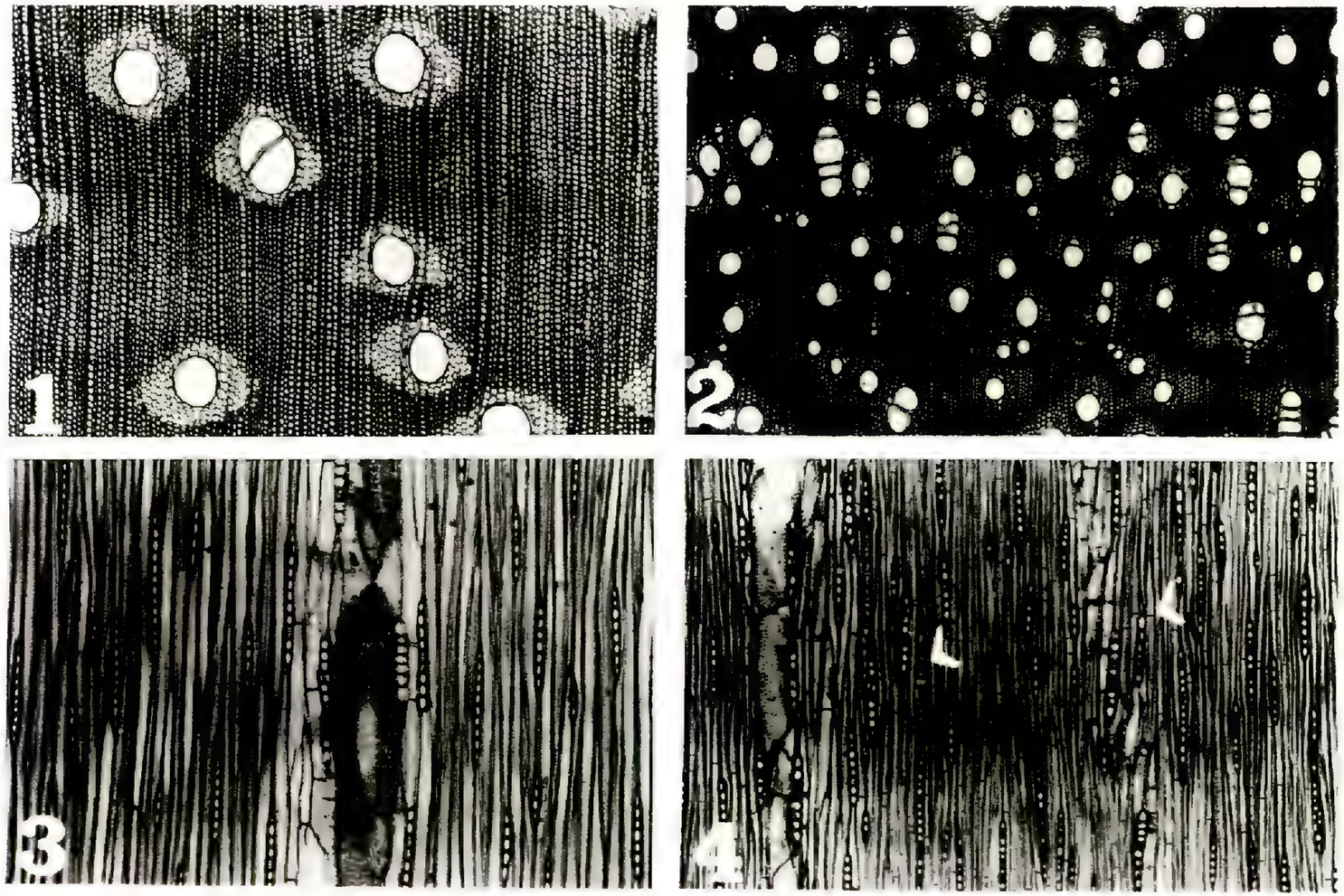
O. Heartwood yellow-brown. . . . . *Chloroleucon.*
O. Heartwood red-brown. . . . . .
. . . . . *Pithecellobium* (sensu stricto).

ANATOMICAL DESCRIPTIONS

TABLE 2 summarizes the important anatomical characters for each wood type, and FIGURES 1–8 illustrate typical anatomical characteristics of the *Pithecellobium* complex. Complete descriptions of the individual wood types are given below. TABLE 3 lists the physical characters that are often of value in wood identification. The different heartwood colors referred to in the descriptions are illustrated by a color photo in Cassens (1973).

Pithecellobium s.l., including *Albizia,* is characterized by several features that do not vary significantly among the different wood types. These characters are not repeated in the wood descriptions. A general description of *Pithecellobium* s.l. is as follows: Heartwood light yellow, yellow-brown, red-brown, and dark brown to light brown with dark stripes. Specific gravity 0.52–1.09; fluorescence yellow, very pale yellow, or negative; froth test positive, short positive, or negative; growth increments more or less demarcated by fine bands of marginal parenchyma or by flattened cells. Wood diffuse porous; pores few to moderately numerous (3 to 17/sq. mm.), generally distinct without aid of a hand lens except in *Chloroleucon, Ebenopsis, Klugiodendron,* and *Zygia*; diameter moderately small to moderately large (78–273 μm.). Vessel elements very short to medium sized (217–437 μm.); perforation plates simple with mostly transverse to oblique end walls; intervascular pitting alternate, vestured, and minute, very small, or medium sized (3–10 μm.). Rays homocellular, extremely fine to fine (1 to 5 cells wide, or 12–38 μm.), generally uniseriate, many specimens occasionally biseriate in part, in some wood types consistently 3 to 5 cells wide; height extremely low (11 to over 20 cells, or 177–405 μm.). Paratracheal parenchyma vasicentric to confluent; apotracheal parenchyma sometimes diffuse or in marginal bands; integumented, chambered, rhomboidal crystals often in long chains. Yellow to brown, nonbirefringent compound occasionally to frequently present in portions of the vessels and ray cells of all wood types except *Albizia, Klugiodendron,* and *Macrosamanea*; vessels and rays of the *Ebenopsis* wood-type completely occluded with this compound. Fibers moderately short to medium sized (728–1355 μm.), septate or nonseptate; pits simple and inconspicuous.

Abarema wood-type (51 specimens, 20 species). Sapwood yellowish white, distinct; heartwood red-brown. Specific gravity 0.64; fluorescence yellow, very pale yellow, or negative; froth test positive except for *Pithecellobium villiferum* (SJRw 44177) and *P. mataybifolium* (SJRw 50101). Pores 71 percent solitary, mostly few to sometimes moderately few, 2 (to 4) to 7/sq. mm.; diameter medium sized to very large, mostly moderately large, 154(–222)–316 μm. Vessel elements moderately short to medium sized, 281(–437)–667 μm.; intervascular pitting small, 5–6 μm., apertures sometimes coalescent. Rays mostly uniseriate to sometimes biseriate, 10(–14)–17 μm. wide; average height 12 to over 20 cells, 204(–310)–458 μm. Paratracheal parenchyma mostly



FIGURES 1–4. Anatomical characteristics typical in *Pithecellobium* complex: 1, *Abarema jupunba* (SJRw 49510), transverse section, vasicentric to aliform paratracheal parenchyma, medium-sized to moderately large pores, × 21; 2, *Havardia pallens* (MADw 18342), transverse section, medium-sized pores, growth increments poorly defined by flattened, thick-walled fibers, × 21; 3, *A. jupunba* (SJRw 49510), tangential section, uniseriate rays, longitudinal parenchyma surrounding vessel, nonseptate fibers, × 53; 4, *H. pallens* (MADw 18342), tangential section, septate fibers (right arrow), crystalliferous strands (left arrow), × 53.

TABLE 2. **Anatomical characters of wood types.**

Paratracheal parenchyma*	Vessel elements: Length (μm.)	Vessel elements: Pores: Diameter (μm.)	Vessel elements: Pores: No./sq. mm.	Vessel elements: Pores: Solitary (%)	Intervascular pit diameter (μm.)	Fibers: Length (μm.)	Fibers: F/V†	Fibers: Septate	Rays: Width (μm.)	Rays: Width (in cells)	Rays: Height (μm.)	Rays: Height (in cells)
					ABAREMA (51)‡							
Vas.- ali.; rarely conf.	437	222	4	71	5-6	1,193	2.7	-	14	1(2)§	310	12-20+
					ALBIZIA (16)							
Vas.- ali.	376	210	5	71	6-8 (8-10)	1,031	2.7	+	37	2-4 (1-5)	405	20+
					ARTHROSAMANEA (9)							
Vas.- ali.; some conf.	323	165	5	65	6-8	1,113	3.5	+	38	2-4 (1-5)	371	20+
					CHLOROLEUCON (22)							
Vas.- ali.; rarely conf.	218	131	10	74	6-7	728	3.3	-	12	1 or b‖ (2-3)	248	14-20+
					COJOBA (26)							
Vas.- ali; some conf.	324	171	7	60	3-5	1,072	3.3	-	15	1 or b (2)	298	12-20+

TABLE 2. **Anatomical characters of wood types** (*continued*).

Paratracheal parenchyma*	Vessel elements: Length (µm.)	Vessel elements: Pores: Diameter (µm.)	Vessel elements: Pores: No./sq. mm.	Vessel elements: Pores: Solitary (%)	Intervascular pit diameter (µm.)	Fibers: Length (µm.)	Fibers: F/V†	Fibers: Septate	Rays: Width (µm.)	Rays: Width (in cells)	Rays: Height (µm.)	Rays: Height (in cells)
					EBENOPSIS (3)							
Vas.- ali; some conf.	228	129	17	50	6-7	855	3.7	-	12	1 or b (2)	297	20+
					HAVARDIA (7)							
Vas.-; rare conf. bands	293	144	12	75	6-8	874	3.0	+	13	1 (b)	347	20+
					KLUGIODENDRON (2)							
Vas.- conf.	354	78	12	72	5-6	1,006	2.8	-	12	1 (b)	177	11
					MACROSAMANEA (6)							
Ali.- conf.	350	138	8	58	5-6	926	2.7	+	14	1	246	13-20+
					MARMAROXYLON (15)							
Vas.- mostly ali., conf.	423	189	3 (6)	69	5-7	1,355	3.2	-	13	1 or b (2)	360	20+

					PITHECELLOBIUM (SENSU STRICTO) (37)							
Vas.- ali.; some conf.	265	129	14	73	6-8	745	2.8	+¶	13	1 or b	243	10-20+
					PSEUDOSAMANEA (12)							
Vas.- ali.	319	237	3	58	6-8 (9)	958	3.0	-	15	1 or b (2)	251	17
					PUNJUBA (1)							
Vas.- rarely ali. or conf.	382	273	4	78	6-7	1,108	2.9	-	15	1 (b)	300	14
					SAMANEA (16)							
Vas.- ali.	319	245	3	68	7-10	984	3.1	-	29	1-2 (3)	292	15-20+
					ZYGIA (42)							
Vas.- mostly ali., conf.	356	138	7	69	5-7	1,126	3.2	-	12	1 or b (2)	300	15-20+

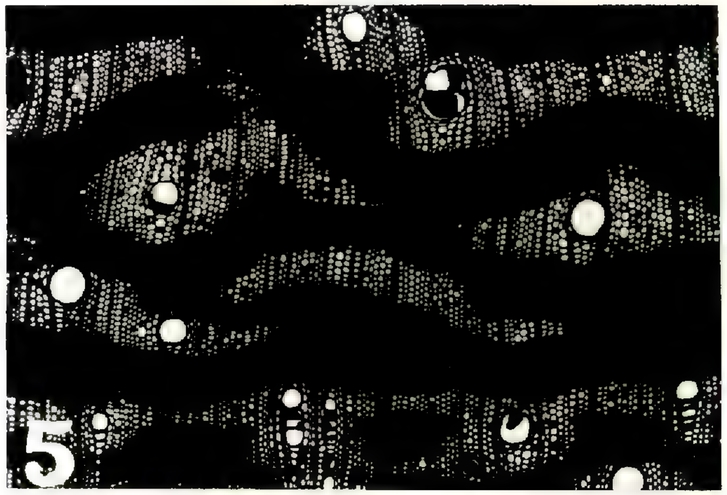
* Vas. = vasicentric; ali. = aliform; conf. = confluent.
† Fiber length/vessel element length.
‡
† Number in parentheses is the number of specimens examined.
§ Number in parentheses indicates that the size occurs sporadically.
// "b" indicates the presence of rays biseriate in part only.
¶ The presence of abundant gelatinous fibers severely reduces the number of septa present.

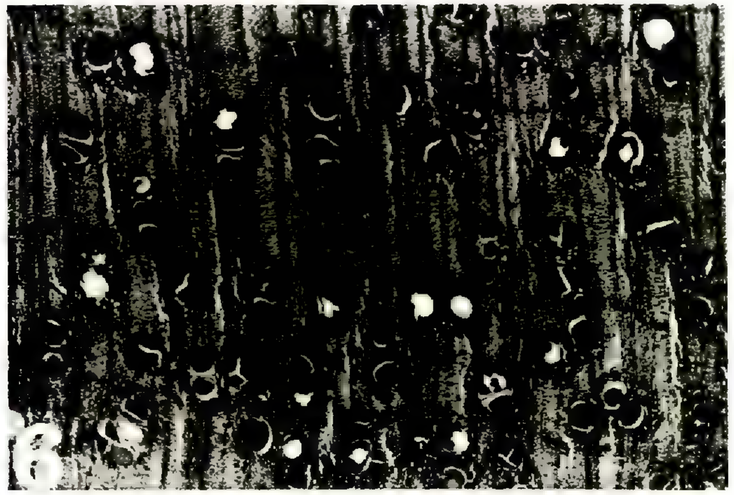
TABLE 3. **Physical characters of wood types.**

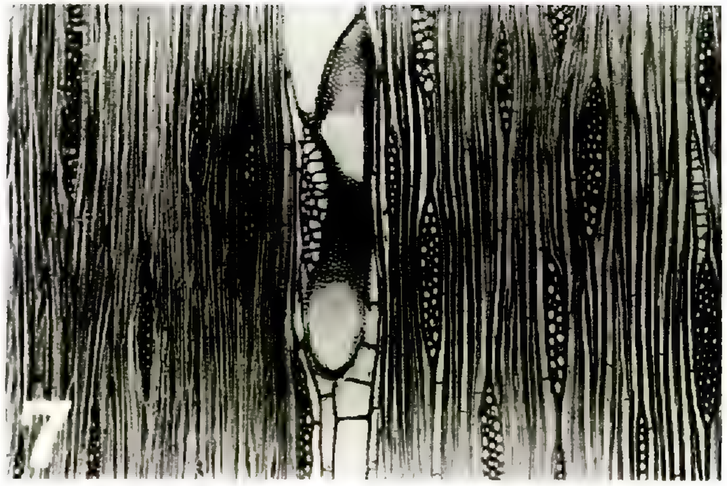
Wood type	Specific gravity*	Heartwood color	Froth†	Fluorescence‡
Abarema	0.64	Red-brown	+, rarely -	Negative to yel. to v.p. yel.
Albizia	0.68	Light yellow	- or short +	Negative
Arthrosamanea	0.67	Light brown	- or short +	Yel. to v.p. yel.
Chloroleucon	0.65	Yellow-brown	-	V.p. yel.
Cojoba	0.68	Red-brown	+ or short +	V.p. yel.
Ebenopsis	1.09	Dark brown	-	Bright yel.
Havardia pallens	0.52	Red-brown	- or short +	Negative to v.p. yel.
Havardia sp. (except H. pallens)	0.87	Dark brown	- or short +	Bright yel.

Klugiodendron§	0.77	--	--	--
Macrosamanea§	0.80	--	--	--
Marmaroxylon	1.00	Light brown with dark stripes	- or short +	Negative
Pithecellobium (sensu stricto)	0.89	Red-brown	-	Negative to v.p. yel.
Pseudosamanea	0.58	Red-brown	+	Bright yel.
Punjuba	0.56	Light yellow	+	Negative
Samanea	0.52	Dark brown	- or short +	Yel. to v.p. yel.
Zygia	0.82	Light yellow	- or short +	Negative

* Oven-dry weight and volume at 5% moisture content.
† + = positive; - = negative.
‡ Yel. = yellow; v.p. yel. = very pale yellow.
§ Specimens small and without apparent heartwood. Also, limited number of specimens.







FIGURES 5–8. 5, *Marmaroxylon racemosum* (SJRw 20720), transverse section, aliform to mostly confluent parenchyma and very thick-walled fibers, × 21; 6, *Ebenopsis flexicaulis* (MADw 25290), transverse section, pores and parenchyma occluded with amorphous compound, × 21; 7, *Albizia colombiana* (SJRw 22478), tangential section, rays 2 or 3 cells wide, septate fibers, alternate intervascular pitting, × 53; 8, *Havardia pallens* (MADw 18342), radial section, showing homogeneous procumbent rays, crystalliferous chains, and septate fibers, × 53.

vasicentric to aliform, rarely confluent; apotracheal parenchyma diffuse or sometimes forming marginal bands. Fibers mostly medium sized to moderately long, 948(–1193)–1680 μm., nonseptate.

Albizia wood-type (16 specimens, 6 species). Sapwood light yellow; heartwood sometimes slightly darker, not sharply demarcated. Specific gravity 0.68; fluorescence negative; froth test negative, occasionally short positive. Pores 71 percent solitary, few to moderately few, 3 (to 5) to 8/sq. mm.; diameter medium sized to moderately large, 152(–210)–261 μm. Vessel elements moderately short to mostly medium sized, 315(–376)–512 μm.; intervascular pitting mostly small, 6–8 μm., rarely medium sized (8–10 μm. in *A. tomentosa*), apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 to 4, rarely 1 or 2, 12(–37)–65 μm.; 20 or more cells high, 219(–405)–776 μm. Marginal ray cells in *A. adinocephala* often containing crystals. Paratracheal parenchyma vasicentric to aliform; apotracheal diffuse parenchyma occasional or absent, fine marginal bands occasionally present. Fibers moderately short to mostly medium sized, 765(–1031)–1296 μm., septate, septa sometimes scarce and difficult to observe.

Arthrosamanea wood-type (9 specimens, 2 species). Sapwood white; heartwood light brown, not sharply demarcated. Specific gravity 0.67; fluorescence yellow to very pale yellow; froth test negative or short positive. Pores 65 percent solitary, few to moderately few, 3 (to 5) to 7/sq. mm.; diameter mostly medium sized, few moderately large, 111(–165)–250 μm. Vessel elements mostly moderately short to medium sized, 252(–323)–436 μm.; intervascular pitting mostly small, 6–8 μm., apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 or more, 29(–38)–63 μm.; 20 or more cells high, 237(–371)–446 μm. Marginal ray cells rarely containing crystals. Paratracheal parenchyma mostly vasicentric to aliform, sometimes confluent; apotracheal parenchyma rarely diffuse, sometimes with interrupted fine marginal bands. Fibers mostly medium sized, rarely moderately long, 990(–1113)–1323 μm., septate, areas without septate fibers common, presence of gelatinous fibers seemingly precluding development of septate fibers.

Chloroleucon wood-type (22 specimens, 7 species). Sapwood yellowish white, distinct; heartwood yellow-brown turning darker upon exposure. Specific gravity 0.65; fluorescence very pale yellow; froth test mostly negative. Pores 74 percent solitary, moderately few to moderately numerous, 5 (to 10) to 15/sq. mm.; diameter moderately small to mostly medium sized, 96(–131)–187 μm. Vessel elements extremely to moderately short, mostly very short, 164(–218)–266 μm.; intervascular pitting small, 6–7 μm., apertures sometimes coalescent. Rays mostly uniseriate, occasionally biseriate, 8(–12)–15 μm. wide (except *C. vinhatico*, where they are commonly 2 or 3 cells wide, or 27 μm.); average height 14 to over 20 cells, 148(–248)–359 μm. Paratracheal parenchyma mostly vasicentric, sometimes short aliform, rarely confluent toward end of growth increment; apotracheal diffuse parenchyma common, marginal bands usually present. Fibers mostly very to moderately short, rarely medium sized, 574(–728)–924 μm., nonseptate.

Cojoba wood-type (26 specimens, 7 species). Sapwood white or often with a brownish cast, giving the appearance of gradual transition between heartwood and sapwood; heartwood red-brown occasionally with isolated sapwood zones. Specific gravity 0.68; fluorescence generally very pale yellow in certain areas, brighter within vessels; froth test varying, usually positive or short positive, sometimes negative. Pores 60 percent solitary, few to moderately numerous, often moderately few, 3 (to 7) to 13/sq. mm.; diameter mostly medium sized to moderately large, 99(–171)–238 μm. Vessel elements moderately short to medium sized, 255(–324)–497 μm.; intervascular pitting very small to minute, 3–5 μm., mostly 4 μm., apertures sometimes coalescent. Rays mostly uniseriate, commonly biseriate in some specimens, 12(–15)–30 μm. wide; average height 12 to over 20 cells, 201(–298)–424 μm.; storied in localized areas. Paratracheal parenchyma always vasicentric to aliform, sometimes forming narrow, confluent bands; apotracheal diffuse parenchyma common, often with conspicuously large cells, marginal bands sometimes present. Fibers moderately short to mostly medium sized, 810(–1072)–1451 μm., nonseptate.

Ebenopsis wood-type (3 specimens, 1 species). Sapwood yellowish white, distinct; heartwood dark brown, oily to touch. Specific gravity 1.09; fluorescence yellow; froth test negative. Pores 50 percent solitary, moderately numerous to numerous, 14 (to 17) to 21/sq. mm.; diameter medium sized, 114(–129)–141 μm. Vessel elements very short, 208(–228)–239 μm.; intervascular pitting small, 6–7 μm., apertures occasionally coalescent. Rays mostly uniseriate, occasionally biseriate in some specimens, 10(–12)–13 μm. wide; usually 20 or more cells high, 258(–297)–361 μm. Paratracheal parenchyma mostly vasicentric to aliform, sometimes short confluent; apotracheal parenchyma diffuse, marginal bands usually present. Fibers moderately short, 799(–855)–889 μm., nonseptate.

Havardia wood-type (7 specimens, 3 species). Sapwood yellowish, distinct; heartwood red-brown in *H. pallens*, dark brown in *H. platyloba*. Specific gravity of *H. pallens* 0.52, all other species 0.87; fluorescence in *H. pallens* negative or with pale yellow streaks, in *H. platyloba* bright yellow; froth test negative or short positive. Pores 75 percent solitary, moderately few to moderately numerous, 10 (to 12) to 16/sq. mm.; diameter medium sized, 118(–144)–169 μm. Vessel elements very short to medium sized, 246(–293)–354 μm.; intervascular pitting small to medium sized, 6–8 μm., apertures sometimes coalescent. Rays mostly uniseriate or biseriate in part, 10(–13)–15 μm. wide; 20 or more cells high, 307(–347)–412 μm. Paratracheal parenchyma mostly vasicentric, rarely forming short, confluent bands; apotracheal parenchyma sometimes diffuse, marginal bands present. Fibers moderately short to medium sized, 766(–874)–1068 μm., septate.

Klugiodendron wood-type (2 specimens, 1 species). Wood yellow to white, heartwood and sapwood not distinguishable on available material. Specific gravity 0.77; fluorescence negative; froth test positive. Pores 72 percent solitary, moderately numerous, 12/sq. mm.; diameter moderately small, 78 μm. Vessel elements barely medium sized, 354 μm.; intervascular pitting

small, 5–6 μm. Rays uniseriate, rarely biseriate in part, 12 μm. wide; average height 11 cells, 177 μm. Paratracheal parenchyma vasicentric to confluent; apotracheal parenchyma diffuse. Fibers medium sized, 1006 μm., nonseptate. A third specimen (*Ll. Williams 4190,* MADw 15942) had septate fibers, in contrast to the others, and appeared to be from a tree buttress. It is, therefore, not included in the anatomical description but is listed in the specimens examined.

Macrosamanea wood-type (6 specimens, 5 species). All specimens branchlike, less than 3 cm. in diameter, without apparent heartwood; all wood yellow to white except that of *M. simabifolia,* which is light brown. Specific gravity 0.80; fluorescence negative; froth test negative or short positive. Pores 58 percent solitary, moderately few, 7 (to 8) to 10/sq. mm.; diameter medium sized, 117(–138)–153 μm. Vessel elements moderately short to medium sized, 279(–350)–420 μm.; intervascular pitting small, 5–6 μm. Rays uniseriate, 12(–14)–15 μm. wide; 13 to over 20 cells high, 222(–246)–280 μm. Paratracheal parenchyma mostly aliform or confluent; apotracheal diffuse parenchyma scarce or absent, marginal bands present. Fibers moderately short to medium sized, 797(–926)–1021 μm., septate. Specimens examined contained gelatinous fibers, making observation of nongelatinous septate fibers difficult.

Marmaroxylon wood-type (15 specimens, 5 species). Sapwood not demarcated; heartwood distinctive due to dark stripes 5–25 mm. wide (heartwood in *Pithecellobium basijugum* solid dark brown). Specific gravity 1.00; fluorescence negative; froth test negative or short positive. Pores 69 percent solitary, few, 3/sq. mm. in *M. racemosum,* to moderately few, 6/sq. mm. in other species; diameter mostly medium sized to moderately large, 107(–189)–242 μm. Vessel elements moderately short to mostly medium sized, 268(–423)–548 μm.; intervascular pitting small, 5–7 μm., apertures occasionally coalescent. Rays uniseriate or biseriate, uniseriates 10(–13)–22 μm. wide, biseriates 24 μm.; 20 or more cells high, 207(–360)–500 μm. Paratracheal parenchyma vasicentric to mostly aliform or short confluent; apotracheal diffuse parenchyma scarce, fine marginal bands present. Fibers mostly medium sized to moderately long, 1066(–1355)–1666 μm., nonseptate.

Pithecellobium (sensu stricto) wood-type (37 specimens, 7 species). Sapwood yellowish white; heartwood red-brown; transition sometimes gradual. Specific gravity 0.89; fluorescence negative or very pale yellow, but conspicuous in the vessel lumens; froth test negative. Pores 73 percent solitary, moderately few to numerous, mostly moderately numerous, 6 (to 14) to 33/sq. mm.; diameter moderately small to moderately large, mostly medium sized, 98 (–129)–218 μm. Vessel elements very short to medium sized, mostly moderately short, 209(–265)–338 μm.; intervascular pitting small to medium sized, 6–8 μm., apertures sometimes coalescent. Rays mostly uniseriate, in some specimens rarely biseriate or triseriate, uniseriates 10(–13)–15 μm. wide, biseriates and triseriates 25 μm.; average height 10 to slightly over 20 cells, 160(–243)–428 μm. Paratracheal parenchyma vasicentric to slightly aliform, sometimes forming confluent bands; apotracheal parenchyma diffuse, marginal

bands common. Fibers very short to medium sized, mostly moderately short, 572(–745)–922 μm. Some specimens conspicuously septate while others not obviously so, apparently due to gelatinous fibers. Four wood specimens of *P. dulce* (SJRw 49282, SJRw 10058, MADw 13887, and MADw 5122) are coarser textured, with wider, higher rays, and lower specific gravity. These differences are probably the result of faster growth and are considered species variation.

Pseudosamanea wood-type (12 specimens, 2 species). Sapwood light gray, distinct; heartwood red-brown. Specific gravity 0.58; fluorescence bright yellow; froth test positive. Pores 58 percent solitary, mostly few, 2 (to 3) to 5/sq. mm.; diameter medium sized to very large, mostly moderately large, 182(–237)–299 μm. Vessel elements mostly moderately short to medium sized, 283(–319)–369 μm.; intervascular pitting small to medium sized, 6–8 μm., apertures sometimes coalescent. Rays mostly uniseriate, occasionally biseriate, uniseriates 12(–15)–16 μm. wide, biseriates 30 μm.; average height 17 cells, 216(–251)–343 μm., storied rays occasional in localized areas. Paratracheal parenchyma mostly vasicentric, sometimes short aliform; apotracheal diffuse parenchyma scarce, marginal bands rare. Fibers mostly medium sized, sometimes moderately short, 846(–958)–1105 μm., nonseptate.

Punjuba wood-type (1 specimen). Wood light yellow; heartwood and sapwood not distinguishable; sample probably all heartwood. Specific gravity 0.56; fluorescence negative; froth test positive. Pores 78 percent solitary, few, 4/sq. mm.; diameter moderately large, 273 μm. Vessel elements medium sized, 382 μm.; intervascular pitting small, 6–7 μm. Rays uniseriate, 15 μm. wide; average height 14 cells, 300 μm. Paratracheal parenchyma mostly vasicentric to rarely short aliform or confluent; apotracheal parenchyma sometimes diffuse. Fibers medium sized, 1108 μm., nonseptate.

Samanea wood-type (16 specimens, 1 species, 1 variety). Sapwood white to light gray, distinct; heartwood dark brown. Specific gravity 0.52; fluorescence yellow to very pale yellow; froth test generally negative, sometimes short positive. Pores 68 percent solitary, few, 2 (or 3) to 5/sq. mm.; diameter medium sized to very large, mostly moderately large, 152(–245)–312 μm. Vessel elements very short to medium sized, mostly moderately short, 227(–319)–366 μm.; intervascular pitting medium sized, 7–10 μm., apertures sometimes coalescent. Rays uniseriate to triseriate, mostly biseriate, biseriates 25(–29)–35 μm. wide; average height 15 to over 20 cells, 207(–292)–473 μm. Marginal ray cells occasionally containing crystals. Paratracheal parenchyma mostly vasicentric, sometimes short aliform; apotracheal parenchyma diffuse, occasionally forming very narrow bands. Fibers moderately short to mostly medium sized, 721(–984)–1288 μm., nonseptate.

Zygia wood-type (42 specimens, 15 species). Wood light yellow, heartwood not demarcated; pith flecks common, resulting in small, brown markings; brownish-colored wood sometimes around pith and knots. Specific gravity 0.82; fluorescence negative; froth occasionally short positive, otherwise negative. Pores 69 percent solitary, few to moderately numerous, mostly

moderately few, 3 (to 7) to 15/sq. mm.; diameter moderately small to moderately large, mostly medium sized, 86(–138)–207 μm. Vessel elements very short to medium sized, 224(–356)–492 μm.; intervascular pitting small, 5–7 μm., mostly 6 μm., apertures occasionally coalescent. Rays mostly uniseriate, rarely biseriate, 10(–12)–16 μm. wide; 15 to over 20 cells high, 197(–300) –469 μm. Paratracheal parenchyma vasicentric to mostly aliform and confluent; apotracheal diffuse parenchyma occasional or absent, fine marginal bands present. Fibers moderately short to mostly medium sized, 837(–1126) –1387 μm., nonseptate.

COMPARATIVE ANATOMY OF SECONDARY XYLEM WITHIN PITHECELLOBIUM S.L.

Pithecellobium s.l. is a small part of the relatively large, anatomically specialized subfamily Mimosoideae of the Leguminosae. In a family or subfamily where the secondary xylem is specialized, large variations—particularly in those characters of phylogenetic significance—are generally not found. In the secondary xylem of the *Pithecellobium* complex, notable variations in tracheary element length, perforation plate type, vessel pitting, and ray structure were not observed (TABLE 2). However, based on anatomical characters that do not clearly suggest phylogenetic trends, the woods of *Pithecellobium* can still be divided into four groups, each group containing from one to six different wood types.

The four groups are based on the presence or absence of septate fibers and confluent parenchyma. Group 1 lacks both septate fibers and confluent parenchyma and is composed of the *Chloroleucon, Ebenopsis, Samanea, Pseudosamanea, Cojoba,* and *Abarema* wood-types. Group 2 has septate fibers but lacks confluent parenchyma; it is composed of *Pithecellobium* sensu stricto, *Havardia, Arthrosamanea,* and *Albizia* wood-types. Group 3, which lacks septate fibers but has confluent parenchyma, comprises *Zygia* and *Marmaroxylon* wood-types. Group 4 has both septate fibers and confluent parenchyma and contains only the *Macrosamanea* wood-type.

Although each of the four groups is anatomically distinct, relationships among the different groups are difficult to ascertain. Groups 3 and 4, however, appear to be more closely related than any other combination of groups. Both groups are characterized by confluent parenchyma, uniseriate rays, medium-sized vessel elements, and intervascular pits 5–7 μm. in diameter. Similarities and differences are about the same among the other groups; therefore, relationships cannot be determined. However, the groups provide a convenient context for discussing the characteristics found in each wood type.

GROUP 1 (both septate fibers and confluent parenchyma absent)

The *Cojoba* wood-type has moderately short vessel elements, medium-sized pores, red-brown heartwood, and very small to minute (3–5 μm.) intervascular pits. The minute vessel pitting in this wood type is unique in the *Pithecellobium* complex.

The *Samanea* wood-type has moderately short vessel elements, moderately large pores, biseriate rays, medium-sized (7–10 μm.) intervascular pits, and dark brown heartwood. The intervascular pitting and biseriate rays distinguish this wood type from all others in Group 1.

The *Abarema* wood-type has moderately short to medium-sized vessel elements, moderately large pores, small (5–6 μm.) intervascular pits, mostly uniseriate rays, and red-brown heartwood. This wood type is distinguished from others in Group 1 by the size of the pores and intervascular pits, and by the mostly uniseriate rays.

The *Pseudosamanea* wood-type has moderately short vessel elements, moderately large pores, uniseriate rays, small to medium-sized (6–8 μm.) intervascular pits, and red-brown heartwood. The presence of mostly uniseriate rays and the size of the intervascular pits and pores differentiates this wood type in Group 1.

The *Chloroleucon* wood-type has very short vessel elements, medium-sized pores, small (6–7 μm.) intervascular pits, uniseriate rays, yellow-brown heartwood, and a specific gravity of 0.65. The size of the pores, the color of the heartwood, and the specific gravity separate this wood type in Group 1.

The *Ebenopsis* wood-type has very short vessel elements, medium-sized pores, small (6–7 μm.) intervascular pits, uniseriate rays, dark brown heartwood, vessels filled with an amorphous substance, and a specific gravity of 1.09. This wood type is distinguished by the color of the heartwood and the high specific gravity.

The various wood types in Group 1 are identifiable by relative differences in cell dimensions and macroscopic characteristics. Phylogenetic relationships among the wood types are not clear, but interesting observations are noted.

The vessel element lengths of the *Chloroleucon* and *Ebenopsis* wood-types are nearly the same, but both are shorter than that of any other wood type in the *Pithecellobium* complex. The short vessel element length indicates that the two woods are probably at a higher level of specialization than any others in the *Pithecellobium* complex. Other microscopic features of these woods are nearly identical, and only the macroscopic features vary. Thus, the *Chloroleucon* and *Ebenopsis* woods appear more closely related to each other than to any others in Group 1.

The wood of *Chloroleucon vinhatico* (Record) Record deserves special mention. It has rays two or three cells wide, while those of other species of *Chloroleucon* are uniseriate. Thus, *C. vinhatico* is distinct, but it is maintained in the *Chloroleucon* wood-type because other anatomical characters are similar.

The vessel elements of the *Samanea, Pseudosamanea,* and *Cojoba* wood-types are similar in length, although they are longer than those of *Ebenopsis* and *Chloroleucon* types. The *Cojoba* wood-type has smaller intervascular pits and pores than do the *Samanea* and *Pseudosamanea* types. *Pseudosamanea* and *Cojoba* wood-types have uniseriate rays, whereas the *Samanea* wood-type is biseriate. *Samanea* and *Pseudosamanea* wood-types differ slightly in ray width and intervascular pit diameter. Therefore, the *Samanea* and *Pseudosa-*

manea wood-types appear closely related. The *Cojoba* type does not appear close to any other wood types in Group 1.

The *Abarema* wood-type has the longest vessel elements in Group 1 and is probably at the lowest level of specialization. Differences in vessel element length, intervascular pit diameter, pore diameter, wood color, and specific gravity suggest that the *Abarema* type does not appear closely related to *Ebenopsis, Chloroleucon,* or *Cojoba* wood-types. However, because of similarities of pore diameter and specific gravity, the *Abarema, Samanea,* and *Pseudosamanea* wood-types are somewhat similar.

GROUP 2 (septate fibers present, confluent parenchyma absent)

The wood types of *Albizia* and *Arthrosamanea* are characterized by rays two to four cells wide, vasicentric to aliform parenchyma, medium-sized to moderately large pores, small to medium-sized intervascular pits, moderately short to medium-sized vessel elements, and light yellow to light brown heartwood. These two wood types are discernible from all others in the group by ray width and heartwood color. The woods of *Albizia* and *Arthrosamanea* cannot be separated. They are maintained as two separate wood types on the basis of taxonomic findings.

The *Havardia* and *Pithecellobium* s.s. wood-types have medium-sized pores, small to medium-sized intervascular pits, very short to medium-sized vessel elements, and mostly uniseriate rays. These two wood types appear more closely related to each other than to any others in Group 2. Septate fibers, abundant in *Havardia* and scarce in *Pithecellobium* s.s., separate these two types. Heartwood color and specific gravity also vary among some species, suggesting that *Havardia* and *Pithecellobium* s.s. wood-types are distinct from each other.

Due to differences in ray width, pore diameter, vessel element length, and certain physical characters, the *Albizia* and *Arthrosamanea* wood-types do not appear closely related to the *Havardia* and *Pithecellobium* wood-types. The *Pithecellobium* s.s. and *Havardia* wood-types have shorter vessel elements and narrower rays than the *Albizia* and *Arthrosamanea* wood-types. Thus, the *Pithecellobium* s.s. and *Havardia* wood-types suggest a higher level of specialization within Group 2.

GROUP 3 (septate fibers absent, confluent parenchyma present)

The *Marmaroxylon* and *Zygia* wood-types have medium-sized vessel elements and pore diameters, nonseptate fibers, aliform to mostly confluent parenchyma, small intervascular pits, and mostly uniseriate rays. The heartwood of the *Marmaroxylon* wood-type is light brown with dark stripes, while that of the *Zygia* type is light yellow. The microscopic features of *Marmaroxylon* and *Zygia* wood-types are similar. These two wood types thus appear more closely related to each other than to any other types.

GROUP 4 (both septate fibers and confluent parenchyma present)

The *Macrosamanea* wood-type has moderately short to medium-sized vessel elements, medium-sized pores, small intervascular pits, uniseriate rays, septate

fibers, and aliform to mostly confluent parenchyma. The secondary xylem of the *Macrosamanea* wood-type appears distinct from all others in the *Pithecellobium* complex.

COMPARISON OF WOOD TYPES WITH TAXONOMIC CLASSIFICATION SYSTEMS

The secondary xylem of *Pithecellobium* s.l. may be an aid in developing a taxonomic classification system that more nearly reflects the relationships of this complex genus. Based on variation in the macro- and microscopic wood anatomy, 15 wood types are apparent. For the most part, these 15 types compare favorably with the existing classification systems that have been proposed for *Pithecellobium.*

In 1875 Bentham monographed the New World *Pithecellobium* complex. He did not split *Pithecellobium* into a number of new genera but arranged the species by sections and series (TABLE 4). Many of these sections and series are treated as genera by current taxonomists. Several of the species studied by Bentham are obscure today: their names do not appear in recent literature, and wood specimens are unavailable. Therefore, some recently proposed species names could be synonyms for those in Bentham's monograph.

In TABLE 4 the various wood types are aligned with the corresponding sections and series proposed by Bentham (1875). Eight species in the *Abarema* wood-type, one in *Arthrosamanea,* three in *Chloroleucon,* two in *Havardia,* three in *Macrosamanea,* five in *Pithecellobium* s.s., and nine in *Zygia* were known to Bentham and correspond directly with the section and series as indicated. However, the only species in the *Samanea* wood-type (*Samanea saman* (Jacq.) Merr.) and one of seven species in the *Cojoba* wood-type (*Pithecellobium* (*Cojoba*) *sophorocarpum* (Bentham) Britton & Rose) also appear in series 2, Carnosae. *Klugiodendron laetum* (Poeppig & Endl.) Britton & Killip appears in section *Abaremotemo,* but observations of the secondary xylem suggest that *K. laetum* belongs in its own wood type, *Klugiodendron. Clypearia* is from the Old World and is thus not considered in this investigation. With few exceptions, the secondary xylem can be used as a basis to form the same groups that Bentham proposed as sections and series.

The *Pseudosamanea, Arthrosamanea, Cojoba,* and *Ebenopsis* wood-types also contain some species known to Bentham. He placed these species in such widely different genera as *Lysiloma, Mimosa, Acacia,* and *Inga.* Current practice dictates their placement in *Pithecellobium* s.l. or its segregates.

In 1928 Britton and Rose investigated the North and Central American species of *Pithecellobium.* In TABLE 4 their segregate genera are aligned with the various wood types. The *Cojoba, Chloroleucon, Ebenopsis, Havardia,* and *Pithecellobium* wood-types contain seven, four, one, three, and five species, respectively, from Central America, and Britton and Rose listed these same species in the respective genera. The eight Central American species in the *Abarema* wood-type correspond to six species of *Jupunba* and two species of *Samanea.* The *Samanea* wood-type contains one Central American species that Britton and Rose list in *Samanea.* Three of the five

TABLE 4. **Comparison of wood types with two taxonomic classification systems.**

Britton & Rose, 1928	Wood types	Bentham, 1875
	Klugiodendron*	Section 3 Abaremotemo
Jupunba	Abarema	Section 4 Samanea
Samanea	Samanea	Series 1 Subarticulatae
Cojoba	Cojoba	Series 2 Carnosae
Albizia	Albizia†	
	Pseudosamanea	
	Arthrosamanea*	Series 4 Parviflorae
Chloroleucon	Chloroleucon	Section 7 Chloroleucon
Ebenopsis	Ebenopsis	
Havardia	Havardia	Section 5 Ortholobium
	Macrosamanea*	Section 4 Samanea
		Series 3 Coriaceae
Pithecellobium	Pithecellobium	Section 1 Unguis-cati
Zygia	Zygia	Section 6 Caulanthon
	Marmaroxylon*†	
	Punjuba*†	

* Klugiodendron, Arthrosamanea, Macrosamanea, Marmaroxylon, and Punjuba are South American genera and are thus not reviewed by Britton and Rose (1928).

† Species included in the Punjuba, Marmaroxylon, and Albizia wood-types were not known to Bentham (1875).

species reported in *Albizia* by Britton and Rose correspond to the *Albizia* wood-type, and the remaining two to the *Pseudosamanea* wood-type. The *Albizia* wood-type is characterized by rays two to four cells wide, septate fibers, and a light yellow heartwood, whereas the *Pseudosamanea* wood-type has predominantly uniseriate rays, nonseptate fibers, and a red-brown heartwood; thus, these wood types do not appear closely related. The *Zygia* wood-type contains eight species from Central America: six are listed in *Zygia* by Britton and Rose; the other two were not named at the time of their 1928 publication.

With regard to Central American species, there are marked similarities among the wood types and the genera as proposed by Britton and Rose.

There are two exceptions—certain species of *Albizia* are included in the *Pseudosamanea* wood-type, and certain species of *Samanea* are included in the *Abarema* wood-type. A comparison of all species in the *Pithecellobium* complex studied by Bentham (1875) and by Britton and Rose (1928) with those species comprising the various wood types is included in Cassens (1973).

A study of the Mimosaceae and Caesalpiniaceae of Colombia was initiated by Britton and Rose and completed and published by Britton and Killip (1936). They recognized *Abarema, Albizia, Arthrosamanea, Chloroleucon, Cojoba, Havardia, Klugiodendron, Macrosamanea, Pithecellobium, Pseudosamanea, Punjuba, Samanea,* and *Zygia* as distinct genera. Although a limited number of Colombian species were examined in this study, observations of the secondary xylem support Britton and Killip's genera with few exceptions. Too few wood specimens were available to allow an understanding of the *Klugiodendron* and *Punjuba* wood-types. In addition, the *Albizia* and *Arthrosamanea* wood-types appear closely related and cannot be separated.

Mohlenbrock (1963a, 1963b) has reviewed the *Pithecellobium* complex and its segregate genera. His key to the natural genera includes *Albizia, Arthrosamanea, Chloroleucon, Ebenopsis, Havardia, Samanea,* and *Zygia. Pithecellobium* sensu Mohlenbrock contains the New World segregates *Abarema* and *Cojoba. Pseudosamanea* and *Macrosamanea* are listed as synonyms of *Albizia.* On the basis of the secondary xylem, *Albizia* and *Arthrosamanea* wood-types cannot be separated. However, the *Abarema* and *Cojoba* wood-types can be separated from *Pithecellobium,* and the woods of both *Pseudosamanea* and *Macrosamanea* can be separated from *Albizia.* With the exceptions noted, the genera accepted by Mohlenbrock and the proposed wood types correspond.

Hutchinson (1964) notes the taxonomic problems of *Pithecellobium* s.l. and suggests that a monograph be undertaken on a worldwide basis. However, he does cite *Samanea, Albizia, Pseudosamanea,* and *Zygia* as acceptable genera, which agrees with observations concerning the secondary xylem.

In summary, Bentham's monograph recognized six sections and four series in the New World *Pithecellobium* complex. Later taxonomists raised these sections and series to generic status and added other genera. If the secondary xylem is used as a basis, the *Abarema, Chloroleucon, Cojoba, Ebenopsis, Havardia, Macrosamanea, Marmaroxylon, Pithecellobium, Pseudosamanea, Punjuba, Samanea,* and *Zygia* wood-types can be defined. The woods of *Albizia* and *Arthrosamanea* are inseparable. With the exceptions noted, these wood types correspond closely with the various sections and series proposed by Bentham, and the segregate genera proposed by more recent taxonomists.

If the segregates of the *Pithecellobium* complex are to receive common acceptance, taxonomic study and possible transfer of a number of the species examined in this investigation will be required. Several transfers in the *Abarema* wood-type are necessary due to changes in nomenclatural procedure. Britton and Rose (1928) created the genus *Jupunba* and cited *Jupunba jupunba* (Willd.) Britton & Rose as the type species. This name is a tautonym and is thus incorrect according to the *International Code of Botanical Nomenclature,* Article 24.4. Therefore, Britton and Killip (1936) proposed *Abarema* and cited *A. jupunba* (Willd.) Britton & Killip as the type species. All species

with the generic name *Jupunba* should be transferred to *Abarema*. It is our opinion (based on our observations of the xylem anatomy) that the genus *Abarema* should include the following taxa: *Pithecellobium arenarium* Ducke, *P. auriculatum* Bentham, *P. elegans* Ducke, *P. fanshawei* Sandwith, *P. gonggrijpii* Kleinhoonte, *P. langsdorfii* Bentham, *P. leucophyllum* Spruce ex Bentham, *P. mataybifolium* Sandwith, *P. panurense* Spruce ex Bentham, *P. villiferum* Ducke, *Samanea corymbosa* (Rich.) Pittier, *S. leucocalyx* Britton & Rose, *S. macradenia* (Pittier) Britton & Rose, *S. marginata* (Spruce ex Bentham) Pittier, and *S. pedicellaris* (DC.) Killip. Additional species of *Pithecellobium* that appear to belong to other genera (again based on anatomical observation of the xylem) include the following: *P. glabripetalum* H. S. Irwin to *Albizia*; *P. acacioides* Ducke and *P. mathewsii* Bentham to *Chloroleucon*; *P. membranaceum* (Bentham) Schery to *Cojoba*; *P. consanguineum* Cowan to *Macrosamanea*; *P. collinum* Sandwith, *P. dinizii* Ducke, and *P. umbriflorum* Ducke to *Marmaroxylon*; and *P. juruanum* Harms to *Zygia*. Another transfer that might be made based solely on the wood structure is *Albizia cubana* Britton & Wilson to *Pseudosamanea*. Since in most cases the species in question was named by a taxonomist who did not support the segregation of small genera from *Pithecellobium*, the transfers have never been made to the appropriate segregate genera.

SPECIALIZATION OF PITHECELLOBIUM S.L.

Various authors have reported on the significance of the secondary xylem in the determination of phylogenetic relationships. The secondary xylem can be used to determine whether the wood of *Pithecellobium* s.l. is primitive or advanced (specialized) with respect to other species. Advanced (specialized) is a relative term that suggests that a particular wood is at a higher phylogenetic rank than a primitive one.

Pithecellobium s.l. is characterized by very short to moderately long libriform fibers with minute, slitlike simple pits. The vessel elements are very short to medium sized with simple perforation plates, transverse to oblique end walls, and alternate intervascular pitting. The fiber : vessel ratio of the different wood types ranges from 2.7 to 3.9. The pore diameters are moderately small to moderately large and appear circular to oval in cross section. The rays are extremely low in height, extremely fine to fine in width, and homogeneous. Most of the rays are uniseriate or in part biseriate and are without uniseriate wings. A few rays are two to five cells wide. Most woods in the *Pithecellobium* complex are characterized by abundant vasicentric to aliform paratracheal parenchyma. Confluent paratracheal bands are sometimes present. Distinct storied structure does not occur in the complex, but occasional isolated areas exist. These anatomical features indicate that the woods of *Pithecellobium* s.l. are relatively specialized. Features of a primitive xylem do not exist.

Although the woods of *Pithecellobium* s.l. contain only specialized tracheary elements and tissue types, there are statistically significant differences in vessel element and fiber lengths. Differences also exist in both ray width

and parenchyma type. Based on vessel element length, *Abarema* and *Marmaroxylon* wood-types with longer vessel elements suggest a lower level of specialization in the *Pithecellobium* complex, whereas the shorter vessel elements of *Chloroleucon* and *Ebenopsis* suggest a higher level. Based on fiber length, *Chloroleucon* is again the most specialized wood type, whereas *Marmaroxylon* is the least. When all wood types are considered, there is an overlapping of the confidence intervals for vessel element and fiber lengths, indicating a continuum throughout the generic complex.

Most woods in the *Pithecellobium* complex have rays that are uniseriate or partially biseriate. However, the rays in *Samanea, Albizia,* and *Arthrosamanea* are commonly two to four cells wide. Therefore, the ray tissue in these three wood types is less specialized than others in the *Pithecellobium* complex.

SUMMARY AND CONCLUSIONS

The secondary xylem of 83 species of the *Pithecellobium* complex indicates that on the basis of the presence or absence of septate fibers and confluent parenchyma, four distinct wood groups can be defined. Other anatomical characteristics indicate that these four groups can be further divided into 15 wood types: *Abarema, Albizia, Arthrosamanea, Chloroleucon, Cojoba, Ebenopsis, Havardia, Klugiodendron, Macrosamanea, Marmaroxylon, Pithecellobium* s.s., *Pseudosamanea, Punjuba, Samanea,* and *Zygia.* Although the woods of *Arthrosamanea* and *Albizia* are indistinguishable, they are maintained as two separate wood types because of published morphological findings. The woods of *Klugiodendron* and *Punjuba* constitute two additional types; due to insufficient and immature xylarium specimens, they have not been included in the key or discussed in detail.

When the various wood types are compared to the taxonomic classification systems proposed by Bentham (1875) and by Britton and Rose (1928), marked similarities become obvious. Based on the secondary xylem, the various species of the *Pithecellobium* complex fall into groups similar to those proposed by the various taxonomists who prefer the segregation of several small genera from *Pithecellobium.*

Observations of the secondary xylem indicate that 26 species could appropriately be transferred to segregate genera. In addition, name changes from *Jupunba* to *Abarema* are needed due to incorrect nomenclature.

Most anatomical features expressing specialization trends do not vary appreciably within the *Pithecellobium* complex. Therefore, the evolutionary relationships between different wood groups and types are unclear. However, differences in vessel element and fiber lengths and (to a lesser extent) ray width indicate some specialization levels among wood types. Based on vessel element length, the *Abarema* and *Marmaroxylon* wood-types appear at the lowest level of specialization in *Pithecellobium* s.l., whereas the *Chloroleucon* and *Ebenopsis* wood-types appear at the highest. The *Samanea, Albizia,* and *Arthrosamanea* wood-types have wider rays than others in the *Pithecellobium* complex, thereby indicating a lower level of specialization.

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NOMENCLATURAL NOTES ON THE LAURACEAE OF THE LESSER ANTILLES

Richard A. Howard

The following notes were derived from a study of living plants in the West Indies, from herbarium specimens, and from the extensive literature on the family Lauraceae. They will be the basis of a treatment of the family in the pertinent volume of the *Flora of the Lesser Antilles,* now in preparation.

Beilschmiedia Nees

Beilschmiedia pendula (Sw.) Hemsley, Biol. Centr.-Am. **3:** 70. 1887.

Kostermans (1964), Imchanitzkaja (1974), and others credit the combination to Bentham or to Bentham and Hooker (1880, p. 152), where the transfer of taxa was suggested but the combination was not in fact made. Imchanitzkaja (1974, p. 195) has designated the lectotype as *Swartz s.n.* (s), from Jamaica.

Cinnamomum Schaeffer

Cinnamomum Schaeffer (Bot. Exped. 74. 1760) is a *nomen conservandum.* The original spelling of the generic name was *Ciñamomum,* with the macron presumably indicating extra length, so the conserved spelling is *Cinnamomum.* The type species, published in Blume (Bijdr. Fl. Nederl. Indië. 11[e] stuk. 568. 1826), is indicated as "*C. zeylanicum* Blume (*Laurus cinnamomum* Linnaeus)." This is antedated by *C. verum* Bercht. & Presl (Prir. Rostlin. **2:** 36, 37–44. *t. 7.* 1825). The epithet *C. zeylanicum* Breyne is occasionally used in the literature and in some recent annotations. The reference, "Breynius in Ephem. Ac. Nat. Cur. Annua 4: 139, 140. 1676," appears to be pre-Linnaean and so the name is invalid.

Kostermans has combined the genera *Cinnamomum* and *Phoebe* and has made most of the necessary combinations in a paper entitled "The New World Species of *Cinnamomum* Trew" (1961). In this action he has been followed by Imchanitzkaja (1974) and Adams (1972), but not by Allen (1964), Bernardi (1962), or Philcox (1978). I will accept Kostermans's view for the *Flora of the Lesser Antilles.*

Cinnamomum elongatum (Nees) Kosterm. Reinwardtia **8**(10): 21. 1961.

Phoebe elongata Nees emend. Mez, Jahrb. Bot. Gart. Berlin **5:** 203. 1889. Type: without locality, *Vahl,* in Herb. Willd. *7780, folio 2.*

?Phoebe cubensis Nees, Syst. Laur. 120. 1836. Type: Cuba, *Poeppig s.n.* (B).

Cinnamomum cubensis (Nees) Kosterm. Reinwardtia **8**(10): 21. 1961.

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Cinnamomum elongatum and *C. cubensis* have had varying treatments since the original publication, and the bibliographic citations have varied as well. Britton and Wilson (1924, p. 319) apparently were the first authors to combine the two species when they accepted *Phoebe elongata* (Vahl) Nees and placed *P. cubensis* Nees in synonymy; they have been followed by Brooks (1933, p. 225). Most recently, Imchanitzkaja (1974, p. 204) reversed the status of the two names by accepting *P. cubensis* and considering *P. elongata* as a synonym. León and Alain (1951, pp. 186, 187) and Fournet (1978, p. 484) accepted both species, as did Kostermans (1961, p. 21) when he made the new combinations in *Cinnamomum*.

In the original description of *Phoebe elongata*, Nees (1836, p. 116) cited "*Laurus elongata* . . . Vahl in Herb. Willd. No. 7780. Fol. 1, Poeppig 1311." The Poeppig specimen was from Peru and was excluded by Mez (1889), who referred it to *P. triplinervis* (Ruiz & Pavon) Mez (1889, p. 211). This, in effect, would typify *P. elongata* Nees by the remaining specimen cited by Nees, "Vahl in Herb. Willd. 7780. Fol. 1." However, Mez cited this under *P. montana* (Sw.) Griseb., while he typified *P. elongata* Nees emend. Mez by "Vahl in herb. Willd. n. 7780. fol. 2 (nec 1)." The specific characters are not readily identifiable in the microfiche of the Willdenow herbarium, and the correct typification depends on a reexamination of the herbarium material.

Roig and Acuña (in León & Alain, 1951, p. 186) listed "*Laurus elongata* Vahl" as a basionym of *Phoebe elongata*. Kostermans (1964, p. 293) listed *Cinnamomum elongatum* (Vahl ex Nees) Kostermans, with a basionym of "*Phoebe elongata* Vahl ex Nees," although elsewhere (*ibid.*, p. 1276) he also cited *P. elongata* (Vahl) Nees. For *Laurus elongata* Kostermans (*ibid.*, p. 615) cited Vahl ex West, with the reference "Beskriv. af St. Croix 282. 1793." Although Vahl is generally credited with the names used in West's publication, this time the specific name "longifolia" was used without any description, and the name "elongata" did not appear. Vahl's name is not appropriate to the bibliographic reference.

Mez (1889, pp. 182, 202, 203) considered *Phoebe cubensis*, number 26 in his key, as a collective species. *Phoebe elongata* was listed as number 26a but was not included in the key.

Britton and Wilson were the first to combine the taxa, and the accepted name should be *Cinnamomum elongatum* (Nees emend. Mez) Kosterm.

Cinnamomum falcatum (Mez) Howard, comb. nov.

Ocotea? falcata Mez, Jahrb. Bot. Gart. Berlin **5:** 388. 1889. TYPE: Guadeloupe, Duchassaing *s.n.* (B).

Phoebe falcata (Mez) Mez in Urban, Symb. Antill. **2:** 251. 1900, not Miq. Fl. Indiae Batavae **1:** 912. 1858.

Cinnamomum falcatifolium Kosterm. Reinwardtia **8**(10): 21. 1961.

Kostermans recognized that Mez's transfer of *Ocotea falcata* to *Phoebe* was invalid, as a later homonym, but he unnecessarily created a new name in *Cinnamomum*. The transfer of *Ocotea? falcata* Mez as the correct basionym is in order.

Endlicheria Nees

Endlicheria sericea Nees, Linnaea **8:** 38. 1833.

Kostermans (1964, p. 507) and others cited the authority for this binomial as (Hooker ex Nees) Nees and gave *Laurus sericea* Hooker ex Nees as the basionym. In fact, Nees (1836, p. 369) listed as a synonym the unpublished herbarium name attributed to "Hooker in Herb. Arnott." The exclusion of the parenthetical reference is important since the implied basionym would be invalid, having been antedated by *L. sericea* Blume (1826).

Endlicheria sericea Nees is typified by "Sieber Fl. Ins. Trinit. 175" (B), which was probably from Guadeloupe (Brooks, 1933, p. 227). The genus and species are not included in the Trinidad flora by Philcox (1978).

Endlicheria guadaloupensis Mez, Jahrb. Bot. Gart. Berlin **5:** 124. 1889.

Kostermans (1937, p. 547) had placed this species in the synonymy of *Endlicheria sericea* Nees. Fournet (1978, p. 481) thought the species had been overlooked by recent workers. He recognized the taxon, known only from the original collections by Duchassaing, as having larger leaves than *E. sericea.* Abundant recent material clearly shows that Kostermans's conclusion was correct.

Laurus L.

Laurus geminiflora Ham. Prodr. Pl. Indiae Occ. 37. 1825.

Hamilton published a brief, generalized description and stated that he had seen living material on St. Kitts and Jamaica and herbarium material in the collections of Professor Desvaux. However, no specimen has been located in Paris, and the treatment of the Hamilton binomial in the literature is confusing.

Meissner (1864, p. 102) assigned the Hamilton name, with a question mark, to the synonymy of *Goeppertia geminiflora* Meissner. He cited material collected by Martin in British Guiana and by Guillemin (*231*) in Rio de Janeiro, Brazil. One staminate specimen was attributed to the herbarium of Kunth and one to that of de Candolle. Meissner, however, did not cite material by Hamilton or Desvaux. I assume, therefore, that the specific epithet "*geminiflora* Meissn." is a new name and not a transfer or representative of a basionym.

In 1889 Mez (pp. 78, 79) established the new genus *Systemonodaphne* Mez, and the single species, *S. geminiflora* (Meissner) Mez, is based in part (i.e., *Martin s.n.*) on *Goeppertia geminiflora* Meissner. The collection *Martin 45* is identified, but not as to location within the several herbaria cited. *Leprieur 223* and *Poiteau 63, 64,* from British Guiana, were also cited. *Laurus geminiflora* Ham. is cited in synonymy with a question mark.

Kostermans (1936, pp. 754, 755) described the new genus *Phyllostemonodaphne.* He based the single species, *P. geminiflora* (Meissner) Kosterm., on *Goeppertia geminiflora* Meissner, with the type specimen designated as *Guillemin 231.* Kostermans (1936, p. 756) considered *Martin 45* to represent

the monotypic *Systemonodaphne* of Mez, which he felt should be renamed *S. mezii* Kosterm. He concluded, "*Laurus geminiflora* Desvaux in Hamilton, Prodr. Fl. Ind. Occ. (1825) p. 37 does, according to the description, not correspond either with *Phyllostemonodaphne* or with *Systemonodaphne.*" However, in 1964 Kostermans (p. 527) listed "*Goeppertia geminiflora* (Desv.) Meissn." and stated that the basionym is *Laurus geminiflora* Desv. As indicated above, Kostermans must be in error, or the nomenclature of both *Systemonodaphne* and *Phyllostemonodaphne* must be reconsidered. *Laurus geminiflora* Ham. remains an unplaced name of the Antillean flora until herbarium material can be located.

Litsea Lam.

Duss (1897, p. 306) listed "*Tetranthera laurifolia* Jacq., *Litsea sebifera* Pers." as cultivated in the botanical garden at St. Pierre, Martinique, and represented by his own collection *343.* Fournet (1978, p. 499) repeated the reference but did not indicate if the taxon was still under cultivation. Philcox (1978, p. 563) stated that "a specimen of the East Indian *Litsea sebifera* Juss. presumably from the island of Trinidad is located in the National Herbarium at St. Augustine, Herb. Trin. *n. 979,* but no further data are available." Two specimens of Duss (*348, 4094,* and *348, 4095*, both at NY), representing material once cultivated at St. Pierre and noted as escaped, were originally named *Tetranthera laurifolia* Roxb. and are annotated as *Litsea glutinosa* (Lour.) Roxb. The material available can not be properly placed at this time.

Nectandra Rolander and **Ocotea** Aublet

In *The Bahama Flora* (1920), Britton and Millspaugh accepted the genus *Ocotea* Aublet and listed *Nectandra* Rolander in synonymy. Only a single species, *O. coriacea* (Sw.) Britton, was involved, although the three specific names cited in synonymy were in three genera. In his subsequent work with other coauthors on the floras of Cuba, Puerto Rico, the Virgin Islands, and Trinidad, Britton recognized the two genera *Ocotea* and *Nectandra.*

In 1957 Kostermans described the genera and subgenera of the Lauraceae that he proposed to accept in a revision of the family. He recognized *Ocotea* Aublet with three subgenera, one of them subg. *Nectandra* (Rolander) Kosterm. Kostermans noted that the sexual condition of the flower (perfect or unisexual), the attitude of the tepals at anthesis, and the arrangement of the pollen sacs of the anthers (at two levels or in an arcuate row) were not satisfactory generic characters used either singly or in combination. In fact, he found no fruiting or vegetative characters useful in distinguishing the genera.

There has been no consensus to follow Kostermans's action. In studying the Lauraceae of Venezuela, Bernardi (1962) concluded that although the separation of some species of *Ocotea* and *Nectandra* is very difficult, combining the genera did not simplify the problems of nomenclature or the determination of the species. Actually, he found it relatively easy to differentiate between them in the field by quickly glancing at the stamens. Bernardi continued to recognize both *Nectandra* and *Ocotea* in three papers published in 1967 in which he transferred several species from one genus to the other. Allen

(1964, p. 64) maintained two genera and stated, "Eventually, a detailed, monographic study will be made of this group. Possibly future examination of herbarium material not now available, together with field observations and anatomical study, may show them to represent opposite extremes of a single variable genus. Until such time, despite an overlapping of characteristics in some plants, i.e., the occasional indeterminate position of the anther cells which appear to be in obscure arc-formation or approach superposition on two distinct planes, they are considered as separate genera." Allen (1966, p. 226) wrote, "Subsequently Kostermans has seen fit to combine all three genera, *Ocotea, Nectandra* and *Pleurothyrium,* under *Ocotea.* If we accept this reduction the entire taxonomic fabric of the Lauraceae will be further imperiled; for elsewhere in the family there are several instances where reasons equally strong can be found for combining genera hitherto maintained as distinct entities by all students of the Lauraceae."

Most recently, Imchanitzkaja (1974) recognized both *Nectandra* and *Ocotea* and, after reviewing the reaction to Kostermans's lumping, commented (translation by author): "In this work we consider *Nectandra* as a separate genus, although in the future, with the accumulation of more observations, possibly it will be united with *Ocotea.* At this point, we do not have enough material to decide the question of *Nectandra*'s taxonomic position in view of the small amount of work done on the species of *Nectandra* and *Ocotea,* and the absence of essential research on their morphology, anatomy, and embryology."

In reality, the more practical approach for a limited flora such as that of the Lesser Antilles is to unite the genera. The characteristics that have been used to separate them are found only in some of the functional stamens and even then are often difficult to interpret. They are not useful in the field and are more often than not of little value with most herbarium specimens. For many years Dr. C. K. Allen drew meticulous sketches of floral dissections of the Lauraceae she examined. These sketches may be annotated once or several times with the generic names *Ocotea, Nectandra,* and/or *Phoebe,* with or without question marks, indicating that even after a lifetime of work she was unable to establish the genus for a particular specimen. Bernardi (in Kostermans, 1964, p. viii) referred to the many species transfers he contemplated and perhaps completed (Bernardi, 1967a, 1967b, 1967c). The transfer of species from *Ocotea* to *Nectandra* and vice versa by a single author or successive authors clearly indicates uncertainty among the authorities concerning the generic assignment. It suggests that the designation of the genus has often been based on the particular flower that was dissected.

Nees (1836) and Mez (1889), the early monographers on the family, attempted to solve the problem by recognizing a larger number of genera, even suggesting that dioecism was in itself a reliable character at the generic level or for a major division within a genus. In practical work with herbarium specimens, it is difficult to determine if a stamen is functional and producing pollen, or if the pistil is fertile or sterile. Personal observations made in the field suggest that a polygamodioecious condition is common. Some species described as having perfect flowers were seen to produce only one or a very few

fruits per panicle, and such sexual differences of perfect and functionally unisexual flowers can be observed in the inflorescences. A full understanding of these structural differences, and of the localized production of fruit or the heavy, early fall of flowers, will require additional special study.

Some plants of the Lauraceae in the West Indies produce aberrant or monstrous inflorescences and abnormal flowers. The cause of these aberrant forms is not understood, nor is the nature of their development, or their consistency or production on a plant in one season or in successive years. The aberrant inflorescences and flowers seem to occur regularly in some species and never in others. The aberrant inflorescence may be diffuse and may have many small leaves or a superfluity of bracts.

In other plants, by contrast, the aberrant inflorescence may be congested with an abnormal number of bracts, flowers, or floral parts. Since such specimens are gathered in flower, there is no information available on the production of fruit by these abnormal flowers, and no records can be found to indicate if a plant that produces a monstrous inflorescence one year may do the same again. The leaves of stems associated with monstrous inflorescences may also vary from the normal, being larger, thicker, often toothed or lobed, and sometimes with altered venation. Several specimens assigned to *Ocotea eggersiana* show pinnate venation of the stem leaves, but plinervy on the leaves from what may be an abnormal inflorescence.

The characteristic of domatia in the axils of secondary veins has also been used in the classification of species. Present observations from dried specimens suggest that this characteristic is also unreliable. The domatia may be present or absent, lebetiform or marsupiform, and glabrous or barbate on the same leaf or adjacent leaves. A special study is also needed to compare the domatia in fresh and dried leaves.

Although fruit size and shape have been used in descriptions, these characters have not been evaluated satisfactorily by field studies. The fruiting pedicel of *Ocotea* is brightly colored (usually red), and the mature fruit is dark purple or black. The fruit is variously referred to as a drupe or a berry. Although most mature fruits appear to be slightly succulent, there is no indication of a hard endocarp; thus, their classification as one-seeded berries seems more appropriate.

When dry, the fruiting pedicel may be described as terete or clavate, expanding gradually or abruptly into a flat surface, or into a cupular one that is crateriform, cyathiform, or urceolate, with the margin smooth, irregular, or toothed, and the surface smooth or warty. Photographs of fruits taken in the field can be useful in comparing the shape of fresh and dried fruits or pedicels. The nature and amount of variation resulting from drying are not fully appreciated; therefore, the value of pedicel shape in dried specimens remains to be determined for nearly all species from the Lesser Antilles.

The following species, considered in alphabetical order, have been reported from the Lesser Antilles generally either as *Ocotea* or *Nectandra* and merit some comment.

Ocotea alpina R. A. Howard, sp. nov.

Arbor parva 1–3 m. alta, gemmis lanceolato-ellipsoideis sericeo-pubescentibus. Folia alternata, ad apicem ramulorum aliquantum congesta, petiolis 7–13 mm. longis, canaliculatis, laminis in sicco supra nigro-brunneis subtus pallidioribus, utrinque glabris, minute reticulato-venosis, oblongis, ellipticis vel ovato-lanceolatis, 9–12 cm. longis et 3.5–5 cm. latis, ad basin rotundis, ad apicem acutis vel acuminatis, penninervis, nervis ad 6-paribus. Inflorescentia paniculata, ad 7 cm. longa, minute griseo-adpresso-pubescens, pedunculo ad 3 cm. longo. Florum gemmae ad 2.5 mm. longae, perianthio companulato, leviter pubescenti, stamina ser. I et II antheris 1 mm. longis, ovatis vel rectangularibus, filamentis brevibus, pubescentibus, ser. III antheris 1.8 mm. longis, ovatis obtusis biglandulosis, glandulis brevibus filamentis aequalibus; staminodis 0.8 mm. longis triangularibus, filamentis pubescentibus; gynoecio 1.8 mm. longo, ovario ellipsoideo glabro stylo crasso longiore, stigmate dilatato vel gynoecio nullo. Fructus ellipsoideus, ad 2.5 cm. × 1.2 cm., niger, cupula urceolata, 12 mm. diametro et 5–7 mm. alta, margine plana, pedicello incrassato ad 8 mm. longo, 4 mm. crasso.

TYPE: Guadeloupe, Bois de Nez Cassé, *Duss 3949* (holotype, NY; isotype, GH).

ADDITIONAL COLLECTIONS. **St. Kitts:** Mt. Misery, *J. S. Beard 306* (A, NY), *G. R. Proctor 19207* (A), *19626* (A); Dos d'Ans Pond, *R. A. Howard 11976* (A); Camps Mt., *R. A. Howard & L. I. Nevling 16864* (A); Molyneaux Estate, *Britton & Cowell 696* (NY). **Nevis:** Nevis Peak, *J. S. Beard 457* (NY). **Martinique:** San Martin on Mt. Pelée, *Duss 4411* (NY).

Flowering material of this species has previously been determined as *Ocotea jacquinii* and *Phoebe falcata*. It is clearly distinct from the former in the smaller fruits and glabrous leaves and differs from the latter in the urceolate cupule and in staminal characters.

The specimens *Beard 457, Britton & Cowell 696,* and *Howard & Nevling 16864* are aberrant in having galled flowers in monstrous inflorescences, and stem leaves abnormal in size, shape, and thickness. The galled flowers are aggregated into bracteate clusters and have the perianth parts much thickened. Accessory sterile stamens appear to be formed in all three series in some flowers.

This species occurs in mist forests above 800 meters altitude.

Nectandra antillana Meissner in DC. Prodr. **15**(1): 153. 1864.

In the original description several collections were cited from Cuba, Hispaniola, and Jamaica, in addition to *Belanger 160,* from Martinique, and *Imray s.n.,* from Dominica. Imchanitzkaja (1974, p. 203) stated the lectotype to be "Jamaica, Red Hills, Río Cobre, *Sloane* (BM) (Sloane, 1725, Nat. Hist. Jamaicae 2: 21, tab. 165)."

Bernardi (1962, p. 190, esp. note no. 1) noted that material of this taxon had been called *Nectandra globosa* (Aublet) Mez, *N. pisi* Miq., or *N. glabrescens* Bentham. In 1973 Barneby and Allen annotated material of *N. antillana* as *N. glabrescens* Bentham, and specimens of *N. krugii* Mez as *N.*

globosa (Aublet) Mez. Imchanitzkaja (1974) did not discuss any of these names, but Adams (1972, p. 283) commented under *N. antillana,* "In the strict sense confined to the Greater Antilles and St. Thomas, perhaps also extending to Guadeloupe. *N. globosa* (Aublet) Mez replaces this species in continental America."

Kostermans (1936, pp. 14–19), Bernardi (1962, p. 120), and Allen (1964, p. 118) have discussed this nomenclatural tangle. Although the complete problem will not be solved by my comments, an observation is needed. Both *Nectandra globosa* (Aublet) Mez and *Ocotea globosa* (Aublet) Schlecht. & Cham. appear to be based on *Laurus globosa* Aublet (Hist. Pl. Guiane Fr. 364. 1775). *Laurus globosa* Aublet bears a brief description, "fructu nigro, calice rubente," and reference to "Borbonia fructu globoso, nigro, calice e viridi rubente, Plum. Gen. 4." Lamarck (Encycl. **3:** 451. 1789) cited Aublet and added descriptive material and the references "Plumier Mss. vol. 6, t. 99" and "Sloane Hist. 2 p. 21 t. 166 f. 1." The Sloane reference is to *Trichilia moschata* Sw. (Meliaceae), according to Fawcett and Rendle (Fl. Jam. **4**(2): 211. 1920). The Plumier manuscript reference is important. Kostermans (1936, p. 20) equated Plumier Gen. 4 with "Plumier's plant, figured in Descr. pl. Amer. ed. Burm. (1775) p. 50, t. 60" when he noted that, according to Urban (Repert. Sp. Nov. Beih. **5:** 49. 1920), *plate 60* is identical with *N. antillana* Meissner. He thus came to the conclusion that while the Burman edition does repeat the Plumier *Nova Plantarum* reference and the polynomial, there are, in addition, three synonyms (from Catesby, from Clayton, and from Linnaeus's *Hortus Cliffortianus* and *Species Plantarum*), all of which are today referred to *Persea borbonia* (L.) Sprengel. The illustration (*t. 60*), although crude, is *Nectandra antillana* Meissner, not *Persea borbonia* (L.) Sprengel. Kostermans did not indicate that Urban had made reference to Plumier Mss. Vol. 6, *t. 99* (Repert. Sp. Nov. Beih. **5:** 112. 1920).

The correct name for *Nectandra antillana* Meissner of the Greater Antilles is *Ocotea globosa* (Aublet) Schlecht. & Cham. Despite the citations of Meissner (1864) and Mez (1889) and the general reports of Imchanitzkaja (1974) and Fournet (1978), I have seen no specimens from the Lesser Antilles that should be referred to this species. Herbarium material previously identified as *N. antillana* has proven to be *O. membranacea* (Sw.) Howard. Barneby and Allen's annotations of *N. krugii* Mez as *N. globosa* (Aublet) Mez are not accepted.

Ocotea cernua (Nees) Mez, Mitt. Bot. Vereins Kreis Freiburg **47, 48:** 422. 1888.

Mez published this combination one year preceding his larger paper (1889) that is usually cited as the bibliographic reference. Mez referred only to "Sieber fl. mixt. No. 385," but this can not be regarded as lectotypification since Nees (1836, p. 424) did not cite such a number among the syntypes mentioned in the original description of *Oreodaphne cernua* Nees. Typification of this species requires further study.

Ocotea clavigera Mez, Jahrb. Bot. Gart. Berlin **5:** 239. 1889, Bot. Jahrb. **30**(Beibl. 67)**:** 18. 1901.

Originally Duchassaing and l'Herminier collections from Guadeloupe were cited as in the Berlin and the Barbey-Boissier herbaria. No lectotype has been chosen, and the species is referred to the synonymy of *Ocotea imrayana* Mez.

Ocotea dominicana (Meissner) Howard, comb. nov.

Oreodaphne? dominicana Meissner in DC. Prodr. **15**(1)**:** 139. 1864.
Nectandra dominicana (Meissner) Mez, Jahrb. Bot. Gart. Berlin **5:** 399. 1889.

Syntypes *Imray 173* and *213* were originally cited, and no lectotype has been chosen. The collection *Sieber 229,* from Trinidad, cited by Mez (1889, p. 400) must have a mixed label and must have originated in Guadeloupe (Brooks, 1933, p. 227).

Recent collections have shown that two sizes of leaves are found in this species. Small leaves 8–17 cm. long are usually associated with flowering specimens. Sterile collections or those with detached fruits may have leaves 25–39 cm. long. Field observations on the growth habits of this taxon are needed.

Ocotea dussii Mez, Bull. Herb. Boiss. II. **5:** 241. 1905.

In the original description three collections by Duss (*3888, 4033,* and *4037*) in the herbarium of Krug and Urban (B) were cited. A lectotype should be chosen if the original material still exists at Berlin. I have not seen material of *Duss 3888,* but specimens in other herbaria may bear the numbers *4033, 4037* or *4037, 4033* on one label. I suspect that originally *Duss 4033* was a collection in fruit, and *4037* a collection in staminate flower. Unfortunately, several sheets of *Duss 4037, 4033*—as well as *Duss 2221* and *2221, 3928*—as mounted contain portions of *Ocotea dussii* and of *O. eggersiana,* either as branches or with fruits mixed in the packets. I have found no satisfactory characters for separating the sterile or flowering material currently available of *O. dussii* and *O. eggersiana.* The fruiting cupule of *O. dussii* is flattened or at most 1 mm. deep, and the berries are 2.5 cm. long and 1.5 cm. in diameter. By contrast, *O. eggersiana* has a cupule with an orifice of 5 mm. and a depth of 5 mm. The berries are retained within the cupule and, although immature in all specimens seen, probably will not exceed 1 cm. in length. The choice of a lectotype will be difficult due to the frequent mixture of material.

Ocotea eggersiana Mez, Jahrb. Bot. Gart. Berlin **5:** 363. 1889.

In the original description Mez cited nine collections from four islands represented in eight herbaria, in addition to "*Nectandra exaltata* Griseb. Fl. Brit. W. Ind. 281 in part" for an Imray collection from Dominica. No

lectotype was chosen, and a monographer must assemble the material for proper identification of the mixed collections. Since the species honors Baron von Eggers, it is possible that *Eggers 657* or *988* from Dominica would be a logical choice. However, Eggers collections from Dominica were few, and they were not widely distributed.

Fruiting material was not known at the time of the original publication, and the first description appears to be that supplied by Duss (1897, p. 303) for his collections *2220* and *124,* from Guadeloupe and Martinique, respectively. Possible lectotypification is further complicated by the fact that the species are distinguishable in fruit, but only with difficulty in flower; many collections apparently were mixed in the distribution of duplicates.

Duss (1897) misspelled the specific name as "eggersii" in the text and as "egersii" in the index.

Ocotea l'herminieri Mez (Jahrb. Bot. Gart. Berlin **5:** 273. 1889), known only from the original collection, may be referred to synonymy here.

Nectandra exaltata (Sw.) Griseb. Fl. Brit. W. Indian Is. 281. 1860.

The apparent basionym, *Laurus exaltata* Sw. (Prodr. 65. 1788; Fl. Ind. Occ. **2:** 702. 1800), concerns material from Jamaica. A collector was not cited. Fawcett and Rendle (1914, p. 217) indicated that they had seen a Swartz collection, and they listed *L. exaltata* Sw. in the synonymy of *Nectandra sanguinea* Rolander ex Rottb., now considered to be a species from Surinam. Adams (1978, p. 284) referred "*N. sanguinea* of F. & R. (1914)" to the synonymy of *N. coriacea.* An examination of Swartz's specimens labeled *N. exaltata* in Stockholm and at the British Museum is necessary to settle this problem. Recently, G. R. Proctor has collected material in Jamaica that appears to represent *N. exaltata* as described by Swartz and that seems to be distinct from both *N. sanguinea* and *N. coriacea.*

Nectandra exaltata (Sw.) Griseb. is not represented in the Lesser Antilles. The Imray collection from Dominica cited by Grisebach (1860, p. 281) is *Ocotea eggersiana* Mez.

Mez (1889, p. 456) accepted "*Nectandra exaltata* Gris. (e.p.) Cat. Cub. p. 111 (nec in fl. Br. W. I. Isl. p. 281)" and cited only two collections of Wright from Cuba (*356* (= *2588*) and *1076* (= *2587*)). Apparently Britton was aware of this emended usage by Mez, for Roig and Acuña credited Britton with the new name *N. earlei* Britton ex Roig & Acuña (Rev. Soc. Cuba Bot. **6:** 17. 1949), which must have been obtained from an herbarium annotation. Grisebach (Catal. Pl. Cubens. 111. 1866) cited *N. boniato* Rich. (in Sagra, Cuba Fanerog. ed. 2. **2:** 188. 1859) in synonymy, as did Roig and Acuña. This would appear to be the epithet to be used, rather than the new "earlei" proposed. Kostermans (1964, p. 981) did not explain his parenthetical comment "=Sapotaceae" following the entry of *N. boniato.* Nothing in any of the references given supports this conclusion. No specimens are cited, however, so the typification of *N. boniato* Rich. depends on a search for material from Guanimar, Cuba, in the Paris herbarium.

Imchanitzkaja (1974, p. 204) designated "no. *9616,* Earle (NY, phototypus

sv)'' as the type of ''*Nectandra earlei* Britt. 1949, in Roig y Acuña, l.c.: 17; id. 1951, l.c.: 190.'' There is no reference to Britton (1949) in the bibliography given, and Britton died in 1934. In the herbarium of the New York Botanical Garden there are two collections numbered *9616* made by N. L. Britton, E. G. Britton, and J. F. Cowell on February 26 and 27, 1911, that bear the herbarium name *N. earlei* Britton. However, if this is a new name for *N. exaltata* Griseb., the type should be selected from one of the two Charles Wright collections that Grisebach cited.

Ocotea floribunda (Sw.) Mez, Jahrb. Bot. Gart. Berlin **5:** 325. 1889.

The collection *Duss 111* (NY) has a printed label ''Herbier de la Martinique,'' with Martinique crossed out in pen and Antigua written in by an unknown hand. In fact, the four fragments that comprise the specimen represent *Ocotea floribunda* (Sw.) Mez, *O. imrayana* Mez, and *O. leucoxylon* (Sw.) Mez. *Ocotea floribunda* is known from other collections from Antigua, Montserrat, and Guadeloupe in the Lesser Antilles, but not from Martinique.

Ocotea foeniculacea Mez, Jahrb. Bot. Gart. Berlin **5:** 325. 1889.

Stehlé, Stehlé, and Quentin (Catal. Phanérog. Foug. **2**(3)**:** 122. 1949) reported this species as new to the flora of the French West Indies. No specimens were cited, and the record, which cannot be verified, is questioned. Fournet (1978, p. 486) supplied a description of the taxon and reproduced the illustration originally published by Little, Woodbury, and Wadsworth (Forest Serv., U.S.D.A., Handb. 449. Trees Puerto Rico Virgin Is. *pl. 335.* 1974). The drawing is not a good representation of the species as it is known today based on material from Cuba and Puerto Rico.

Ocotea globosa (Aublet) Schlecht. & Cham. Linnaea **6:** 366. 1831.

See the entry under *Nectandra antillana* for commentary on the recent annotations of specimens as *Ocotea globosa.*

Ocotea l'herminieri Mez, Jahrb. Bot. Gart. Berlin **5:** 273. 1889.

Photographs (NY) have been seen of two sheets in the Boissier herbarium studied by Allen. One (NY Neg. 8476) was labeled ''isolectotype'' in 1970 and appears to have a gall-infected inflorescence. Mez reported the flowers to be perfect, but a drawing of a dissection shows an abortive, pubescent pistil. No recent collections have been associated with this species, which may be referable to *O. eggersiana.*

Ocotea imrayana Mez, Jahrb. Bot. Gart. Berlin **5:** 274. 1889.

A lectotype should be chosen from the collections of *Imray 149* and *335,* cited by Mez from Goettingen and Kew. A number of Duss collections from Guadeloupe and Martinique were labeled ''*Nectandra imrayana* Mez,'' an unpublished name, indicative of the generic problem involved.

Oreodaphne jacquinii Meissner in DC. Prodr. **15**(1): 114. 1864.

In the original description Meissner (1864, p. 114) cited "in Martinicâ (Aquart!). *Laurus martinicensis* Jacq. Coll. 2, p. 109, t. 5 f. 2. Willd., sp. 2, p. 481" and indicated that a specimen was seen in the herbarium of Jacquin. A specimen once in the herbarium at Vienna is represented by Field Museum photograph no. 31205, which clearly shows such a label and the annotation *Ocotea jacquini* Mez. Two of the three leaves in the specimen photographed match in shape and venation the single leaf illustrated by Jacquin in his description of *Laurus martinicensis* Jacq. (Collect. **2:** 109. *t. 5, fig. 5.* 1788). The name *Oreodaphne jacquinii* Meissner is illegitimate since it was superfluous when published.

Ocotea jacquinii Mez, Jahrb. Bot. Gart. Berlin **5:** 422. 1889.

When Mez published *Ocotea jacquinii* (1889, p. 242; as *jacquini*), he cited the illegitimate *Oreodaphne jacquinii* and "*Laurus martinicensis* Jacq. herb. ap. Meissner l.c.," the latter being invalid as an unpublished herbarium name. *Ocotea jacquinii* Mez (corrected spelling) should be regarded as a new name and may be typified by the Aquart specimen in Herb. Jacquin as represented by Field Museum photograph no. 31205 ("*Laurus martinicensis* Jacq. Coll. 2, p. 105 t. 5 f. 2"). Although Mez indicated that Aquart specimens had been seen in herbaria at Copenhagen, Leningrad, and Vienna, none has been cited by recent authors including Bernardi (1967b).

Ocotea krugii (Mez) Howard, comb. nov.

Nectandra krugii Mez, Jahrb. Bot. Gart. Berlin **5:** 422. 1889.

In the original description Mez cited collections in three herbaria: three by Sintenis (*1984, 4004, 6450*) from Puerto Rico, and one by Imray (*214*) from Dominica. No lectotype has been selected, nor should one be before the existing collections are assembled.

Barneby and Allen have annotated sheets of *Nectandra krugii* as *N. globosa* (Aublet) Mez. The correct identity of that taxon has been discussed under *N. antillana* (q.v.). Material called *N. krugii* is distinct, but transfer to *Ocotea* is required.

Ocotea leucoxylon (Sw.) Mez, Jahrb. Bot. Gart. Berlin **5:** 329. 1889.

Credit for this combination has been variously attributed by recent writers to Gomez de la Maza, Bentham, de Lanessan, and Mez.

Bentham (1800, p. 158) reached the conclusion that species of *Oreodaphne* Nees & Martius should be transferred to *Ocotea* Aublet. Bentham mentioned *Oreodaphne leucoxylon* but not the actual combination *Ocotea leucoxylon.*

De Lanessan (Pl. Utiles Colon. Franç. 158. 1886) published the name "*Ocotea leucoxylon* Gr.," which can scarcely be termed a new transfer of the uncited *Oreodaphne leucoxylon* (Sw.) Griseb.

Gomez de la Maza (Dicc. Bot. Nombres Vulg. Cub. Puerto Riq. 12. 1889)

is incorrectly cited as "1888" by Stehlé, Stehlé, and Quentin (1949, p. 120). The exact month and day of its publication are not known. The Mez reference, with a clearly stated basionym, was published August 15, 1889, and is accepted.

Imchanitzkaja (1974, p. 200) has designated as the lectotype "Ind. Occ., *Swartz, sine num.* (s)." Swartz consistently did not cite his own collections in the *Prodromus* and the *Flora*. He did cite the reference "Browne 214.2" in the *Prodromus* (p. 65) and repeated the reference but with a question mark in the *Flora* (**2:** 711). Fawcett and Rendle (Fl. Jam. **3:** 211) also cited Browne with a question mark. It is probable that the Swartz specimen referred to by Imchanitzkaja was collected in Jamaica.

Laurus martinicensis Jacq. Collect. **2:** 109. *t. 5, fig. 2.* 1788.

In the protologue of *Oreodaphne jacquinii* (q.v.), Meissner (1864, p. 114) included this reference and also cited an Aquart specimen from "Herb. Jacquin" bearing the same binomial. Mez (1889) seems to have considered the two items to be distinct, for he referred to the specimen in the protologue of his *Ocotea jacquinii* but included the bibliographic reference in the protologue of *Nectandra martinicensis* Mez (1889, p. 459). I believe that the illustration published by Jacquin and the specimen of Aquart represent one taxon. Therefore, *Laurus martinicensis* Jacq. is a synonym of *Ocotea jacquinii* Mez (not *O. martinicensis* Mez, q.v.).

Nectandra martinicensis Mez

Bernardi (1967b) has discussed this "species," but additional comment is necessary. Bernardi pointed out that Mez (1888) described this taxon in a paper that has been overlooked and that was not cited by Mez in his larger monograph published the following year (1889). In the 1888 paper Mez recognized *Nectandra sanguinea* Rottb. as a "spec. collect." and with it described "subspec. *Nectandra martinicensis* nov. spec." Mez cited the two collections "Sieber, Martinique No. 99; Sutton Hayes, Panama No. 400." In 1889 (p. 459) Mez cited the same collections, this time correcting the location of the Sieber collection to Trinidad and adding a reference to a de Rohr specimen without location. He indicated that these collections had been seen in eleven different herbaria. In the protologue Mez did not cite his 1888 paper but added four references, with the most important being "*Laurus martinicensis* Jacq. Coll. II, p. 109 t. 5 f. 2." Unanswered is the question of the correct bibliographic citation of *N. martinicensis* Mez in 1889. Is this a combination and new status as *N. martinicensis* (Mez) Mez, with the basionym the subspecies published in 1888, or is it a new combination, *N. martinicensis* (Jacq.) Mez, with the Jacquin reference as basionym? Bernardi chose to exclude the Jacquin synonym from the 1889 reference but did not comment on the possible change of rank involved. Bernardi also selected *Sieber 99* from Trinidad in the Geneva herbarium (G) as the lectotype. Further, Bernardi added three species as synonyms of his *N. martinicensis* Mez: *N. tabascensis* Lundell, *N. woodsoniana* Allen, and *N. matudai* Lundell. Thus, *N. martinicensis* Mez *sensu* Bernardi has a range of Mexico, Central America,

Colombia, Trinidad, and Tobago, but not Martinique and doubtfully Montserrat.

Before the correct name for this taxon—considered in the genus *Ocotea*—is suggested, several points require clarification.

Bernardi was not aware of the photograph of the Aquart specimen from the Jacquin herbarium in Vienna (Field Museum photograph no. 31205) that permits the specimen to be recognized as *Ocotea jacquinii* Mez. Bernardi was therefore correct in excluding the Jacquin reference from the definition of *Nectandra martinicensis* Mez and *sensu* Bernardi.

Bernardi's choice of *Sieber 99* (G) as the lectotype must be discussed, since the Sieber collections are known to have unreliable label data. Reference has been made earlier to *Sieber, Fl. Trin. 175* (*Endlicheria sericea*—a species known from Guadeloupe but not from Trinidad). In the present case, the locality of *Sieber, Fl. Martinique 99* was changed by Mez to Trinidad. Brooks (1933, p. 222) indicated that he saw a specimen of *Sieber 99* at Kew, and he listed the species for the flora of Trinidad. More recently, Philcox (1978, p. 582) described the same flora but did not cite the Sieber collection. It should also be noted that Mez (1889, p. 377) cited "*Laurus martinicensis* Sieb. (nec Jacq.) hb. Mart. n. 99" in the synonymy of *Ocotea cernua* (Nees) Mez. It appears that "Sieber 99" is a collection that is mixed taxonomically as well as geographically.

The record from Panama of *Sutton Hayes 400,* cited originally by Mez (1888), was neither cited nor discussed by Allen (1948) in her treatment of the Lauraceae for the *Flora of Panama.* Earlier (1945, p. 381), she had considered *Nectandra martinicensis* to be a species found only in the West Indies; she compared it with *N. woodsoniana* Allen, which she was describing. Bernardi (1967b, p. 72) did see material of *Hayes 400* in five herbaria.

Bernardi (1967b, p. 72) questioned the origin of a Ryan collection without number but supposedly from Montserrat (C). He also cited other collections in the Copenhagen herbarium without collector or location. It is probable that one of these represents the material cited by Mez as having been collected by Rohr. Although Ryan did live and collect in Montserrat, he acquired material from other islands and from Rohr, who collected in Trinidad. Ryan sent his specimens to Vahl in Copenhagen. There is no sound evidence that *Nectandra martinicensis* Mez *sensu* Bernardi occurs in Montserrat, and recent intensive collecting on Montserrat has not revealed the species in that flora.

If the species recognized as *Nectandra martinicensis* Mez by Bernardi and by Philcox (1978) is to be considered as a species of *Ocotea,* a new name is required since Mez published *O. martinicensis* (q.v.) in 1889. The correct name should therefore be:

Ocotea tabascensis (Lundell) Howard, comb. nov.

Nectandra tabascensis Lundell, Lloydia **4:** 48. 1941. TYPE: Mexico, *Matuda 3299.*

Nectandra martinicensis Mez, Mitt. Bot. Vereins Kreis Freiburg **47, 48:** 421. 1888, not *Ocotea martinicensis* Mez (1889). LECTOTYPE: Trinidad, *Sieber 99* (G).

Nectandra woodsoniana Allen, Jour. Arnold Arb. **26:** 380. 1945. TYPE: Costa Rica, *Stork 3059* (FM).
Nectandra matudai Lundell, Wrightia **1/2:** 149. 1946. TYPE: Mexico, *Matuda 4522* (LL).

Ocotea martinicensis Mez, Jahrb. Bot. Gart. Berlin **5:** 270. 1889.

In the protologue Mez cited unnumbered collections of Ryan, Dancer, l'Herminier, and Ponthieu, as well as numbered collections of Imray and Hahn, from Jamaica, Montserrat, Guadeloupe, Dominica, and Martinique. No lectotype has been chosen from the specimens cited, which are deposited in ten different herbaria.

Adams (1972, p. 283) noted that the old records of this taxon from Jamaica based on collections attributed to Dancer and Wright have not been confirmed by recent collections.

Ocotea membranacea (Sw.) Howard, comb. nov.

Laurus membranacea Sw. Prodr. 65. 1788, Fl. Ind. Occ. **2:** 713. 1800.
Nectandra membranacea (Sw.) Griseb. Fl. Brit. W. Indian Is. 282. 1860.

Swartz cited material from Jamaica and Hispaniola. A lectotype (*Swartz s.n.* (s), from Jamaica) was designated by Bernardi (1967b, p. 76).

Most of the material from the Lesser Antilles identified as *Nectandra leucantha* and *N. leucantha* var. *rodiaei* (Schomb.) Griseb. belongs here.

The fruits of this taxon are frequently infected by galls or fungi and become enlarged, rugose, and spongy; they are bright red when fresh. The normal fruits are subglobose, black, and shiny.

Ocotea sanguinea (Rolander ex Rottb.) J. S. Presl

Nectandra sanguinea Rolander ex Rottb. Pl. Surinam. Rar. 11. 1776.

Bernardi (1967a, p. 56) illustrated the holotype specimen (SBT). Many authors have considered this specimen to be lost. I have not been able to verify a bibliographic citation for this combination. The brief entry in *Index Kewensis* is "J. S. Presl, Rostl. ii, 60," and Kostermans (1964) suggested "Presl, Priroz. Rostlinar **2:** 60. 1825." Allen (1945, p. 364) dated the publication as 1846 but could not find the reference and apparently did not discover it in the three volumes of "Prirez. Rostlin." Presumably the binomial is a transfer of *Nectandra sanguinea* to *Ocotea*.

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A MONOGRAPH OF LYONIA (ERICACEAE)[1]

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THE GENUS *Lyonia* Nuttall is an especially fascinating group and is of general biological interest. One is first confronted with the basic question of defining the genus, since *Lyonia* has often been confused with several related genera of the Andromedeae (Ericaceae), especially *Pieris* D. Don, and has sometimes been split into several genera. (This topic has been treated in Judd, 1979.) The genus has never been monographed, although there are various local studies (Small, 1914, 1933; Roig & Acuña, 1957; Handel-Mazzetti, 1936; Fernald, 1950; Anonymous, 1974). However, these treatments have done little to determine phenetic or phylogenetic relationships between taxa. Species of *Lyonia* recognized in the past have been based on characters that are extremely variable within single populations, and even in individual plants. This overdescription of both the West Indian and eastern Asian species has obscured several important ecological, geographic, and morphological patterns.

Lyonia is of phytogeographic interest since it has an eastern Asian–eastern North American disjunction, with an additional center of diversity in the Greater Antilles; one species also occurs in the mountains of eastern and southern Mexico. Therefore, questions concerning the phytogeographic relationships between Asia, eastern North America, Mexico, and the West Indies are discussed. The genus is intriguing from an evolutionary standpoint, since extensive speciation and adaptive radiation have occurred in the Greater Antilles (especially Cuba and Hispaniola), with species occurring at a wide range of elevations, on diverse soil types, and in various vegetation types. Most species of *Lyonia* in this region are narrowly endemic, and many have developed unusual morphological and/or anatomical characteristics.

Phenetic and phylogenetic studies of *Lyonia* and its relatives in the Andromedeae have reaffirmed the generic distinctiveness of *Lyonia* and have clarified relationships among such related genera as *Pieris* D. Don, *Craibiodendron* W. W. Smith, *Agarista* D. Don, and *Agauria* Hooker f. (Judd, 1979). The genus is most easily distinguished by the following characters (here listed in order of importance): prominently thickened capsule sutures; geniculate (or S-shaped) filaments often with two slender and partially disintegrating spurs near the apex; buds frequently with two imbricate scales; inflorescences that overwinter inside the bud; twigs usually with homogeneous pith; minute, wingless seeds with elongated testa cells; leaves with bifacial petiole and/or

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midrib bundles; multicellular hairs with biseriate stalks and large, swollen heads (or heads flattened to form peltate scales); and two more or less opposite bracteoles positioned at or near the base of the pedicel (for further details see Judd, 1979).

The species of *Lyonia* can be grouped into four sections that differ chiefly in structure of their multicellular hairs, in inflorescence type, and in several anatomical features. Sect. PIERIDOPSIS is limited to eastern Asia, sect. LYONIA is most diverse in the West Indies, and sects. MARIA and ARSENOCOCCUS are essentially limited to eastern North America. *Lyonia* is especially diverse in the Greater Antilles, with thirteen species (seventeen taxa) in Cuba, ten (eleven taxa) in Hispaniola, two in Jamaica, and a single one (but two taxa) in Puerto Rico and St. Thomas. Six species (seven taxa) are native to continental North America, and five (thirteen taxa) are found only in eastern Asia. Most species occur in rather sunny environments with acid soils, and species in the West Indies are often limited to mountainous areas.

In the Caribbean the genus has apparently undergone adaptive radiation on each island, with very little exchange of taxa between islands. Within an island the species are often limited to a single mountain range and are usually adapted to specific habitats. The habitats of the generalized species tend to be relatively mesic to slightly xeric, while those of the specialized species are more extreme (e.g., dry white-sand savannas, high-elevation pine forests, or thickets or pine-lands on deep lateritic soils rich in iron oxide, which are developed over serpentine). In the Cordillera Central of Hispaniola, there are pairs of related species (e.g., *Lyonia heptamera* and *L. buchii, L. tuerckheimii* and *L. rubiginosa, L. urbaniana* and *L. tinensis*) with one member in a high-elevation *Pinus occidentalis* forest and the other in a low-elevation pine forest, the two separated by a narrow band of cloud forest at ca. 2000 meters. This pattern is also seen in the Blue Mountains of Jamaica, where *L. octandra* occupies the cloud or elfin forests near the summits and the related *L. jamaicensis* grows on the southern slopes in dry forests at lower elevations. A few Cuban species are also isolated ecologically and altitudinally. Other taxa of Hispaniola (*L. urbaniana* and *L. microcarpa,* for example) are closely related but are geographically isolated because they occur in different mountain ranges. Many Cuban taxa (e.g., the varieties of *L. nipensis,* of *L. obtusa,* of *L. glandulosa,* and of *L. latifolia*) are also geographically isolated. A few species, such as *L. truncata* and *L. microcarpa* (or *L. ferruginea* and *L. fruticosa* of the southeastern United States), seem to be at least partially isolated because they flower at different times.

In contrast to the narrowly endemic species of the Greater Antilles, several species of eastern Asia and the United States (for example, *Lyonia ovalifolia, L. villosa,* and *L. ligustrina*) are very widespread and are usually composed of numerous geographic varieties. *Lyonia ovalifolia* occurs in an arc of over 3500 miles from Japan across China and the Himalayas to northern Pakistan and extends south as far as Thailand, Vietnam, and the Malay Peninsula. These species often spread vegetatively by horizontal underground rhizomes.

In the past six years over 9000 herbarium specimens have been studied, and natural populations of nearly all the taxa of North America, Hispaniola,

Jamaica, and Puerto Rico have been investigated in detail. The species of Cuba and eastern Asia have had to be studied from herbarium material alone. The morphology, anatomy, systematics, ecology, cytology, and geographic distribution of each species have been investigated as thoroughly as possible.

Since the species of *Lyonia* had not been intensively studied in the field, and plants of various geographically or politically separated areas had not been critically compared, the species previously recognized were often highly artificial. The varieties of the widespread Asian species recognized here have often been considered to be distinct species, and slightly different morphological forms—or even identical but geographically separated populations—of the taxa of the West Indies have been similarly treated. These species were often based upon slight differences in leaf shape, the prominence of marginal serrations, or certain indumentum features, but these characters vary within single populations or even within an individual plant. However, many other useful characters such as epidermal lignification and cell shape, venation type, distribution of unicellular hairs, and variation in the morphology of the peltate scales were ignored.

Out of nearly 120 named taxa, 35 species (51 taxa)—including two species and two varieties described for the first time—are recognized here. The species recognized have distinct complexes of morphological characters, geographic ranges, and ecological characteristics.

INFRAGENERIC RELATIONSHIPS

Sectional Relationships

The genus *Lyonia* can be divided into four natural and morphologically distinctive groups, which are recognized in this treatment as sections (see Judd, 1979).

Lyonia sect. Pieridopsis includes *L. ovalifolia, L. villosa, L. chapaënsis, L. macrocalyx,* and *L. compta,* all natives of eastern Asia. These species are characterized by racemose inflorescences; an indumentum of multicellular, long-headed hairs; stems with homogeneous pith; entire-margined, persistent to deciduous leaves usually with unlignified epidermal cells; calyx lobes valvate in bud; filaments usually covered with long, unicellular hairs, at least near the base; two large, imbricate bud scales that often become reddish in autumn; capsules with thickened sutures that usually do not separate as a unit from the adjacent valves in dehiscence; and subapical to more or less central placentae. All of these species except *L. compta* have the floral buds located below the vegetative buds and lack a hypodermis in the leaves. The leaves of all species have bifacial midrib and petiole bundles, although the vascular tissue does not characteristically form a complete ring of xylem (as seen in cross section) within the petiole, as is common in *Lyonia* sect. Lyonia. All species probably spread vegetatively by horizontal underground rhizomes, although as yet this has been documented only for *L. ovalifolia* and *L. villosa.*

Lyonia ovalifolia, L. villosa, and *L. macrocalyx* are probably quite closely related, and all have capsules with more or less prominently thickened sutures,

floral buds borne below the vegetative buds, more or less horizontal to slightly ascending racemes, and semipersistent to deciduous leaves; all lack a leaf hypodermis. *Lyonia compta* appears to be an isolated species that lacks thickened sutures and that has flower buds above the vegetative buds, more or less rigidly ascending racemes, and evergreen leaves with an unlignified adaxial hypodermis. *Lyonia compta* is more similar to the North American *L. ligustrina* in floral bud position and in corolla shape than is any other Asian species. (In *Lyonia* sects. MARIA and ARSENOCOCCUS the floral buds are always positioned above the vegetative buds. In *Lyonia* sect. LYONIA the two bud types are often mixed, but the floral buds tend to develop near the distal end of the branches.) *Lyonia chapaënsis* helps to ally this taxon with the other Asian lyonias, since it also essentially lacks thickened sutures and has very similarly shaped capsules, but has leaves that are morphologically and anatomically very similar to those of *L. ovalifolia*.

Lyonia sect. ARSENOCOCCUS includes the single species *L. ligustrina*, which is native to eastern North America. This taxon is characterized by flowers in complex, paniculate inflorescences; indumentum of multicellular, long-headed hairs; twigs with heterogeneous pith; clearly to only minutely serrulate-margined leaves usually with unlignified epidermal cells; calyx lobes valvate in bud; filaments with long, unicellular hairs near the base; two large, imbricate bud scales that often become reddish in autumn; capsules with thickened sutures that usually do not separate as a unit from the adjacent valves in dehiscence; and placentae positioned more or less subapically. *Lyonia ligustrina* commonly spreads vegetatively by horizontal underground rhizomes. The leaf-midrib bundle is bifacial but does not consistently form a cylinder of xylem within the petiole.

Lyonia sect. MARIA, as defined here, includes two rather distinctive species, *L. mariana* and *L. lucida*. Both are native to eastern North America, although *L. lucida* also occurs in western Cuba. This section is characterized by flowers in fascicles; indumentum of multicellular, short-headed hairs; twigs with homogeneous pith; entire-margined, deciduous (*L. mariana*) or persistent (*L. lucida*) leaves with unlignified or only slightly lignified epidermal cells; calyx lobes valvate in bud; filaments with long, unicellular hairs (*L. mariana*) or merely roughened (*L. lucida*); buds with 2 to 6 (to 8) imbricate scales; and more or less central to nearly basal placentae. The capsular sutures are always strongly thickened and occasionally separate as a unit from the adjacent valves. Both species have conspicuous spurs near the apex of the filaments and spread vegetatively by horizontal underground rhizomes. These two species, although isolated vegetatively, are placed in a single section because of their strong similarities in inflorescence and floral morphology. *Lyonia lucida* is distinctive vegetatively because of its strongly three-angled stems and its very coriaceous, persistent leaves with an intramarginal vein and a unifacial midrib bundle. However, occasional species in other sections (cf., for example, *L. buchii, L. heptamera, L. glandulosa, L. compta*) are anatomically or morphologically peculiar in a few characters, and the few primarily vegetative differences between *L. mariana* and *L. lucida* do not justify placing each in a monotypic section.

Lyonia sect. LYONIA is in many respects the most distinctive subgroup within the genus. It includes *L. ferruginea* and *L. fruticosa,* of the southeastern United States; *L. squamulosa,* of the mountains of eastern and southern Mexico; and 24 species of the Greater Antilles. These species are characterized by flowers in fascicles (or less commonly in short racemes); indumentum of multicellular, peltate scales; stems with a homogeneous pith; entire to irregularly serrate-margined, persistent leaves with epidermal cells strongly lignified (also often with hypodermis lignified); calyx lobes imbricate in bud; filaments merely roughened; buds with two rather small, imbricate bud scales; capsules with prominently thickened sutures usually separating as a unit from the adjacent valves in dehiscence; and more or less subapical placentae. The petiolar vascular bundle of all species is bifacial and characteristically forms a cylinder of xylem and phloem surrounded by a ring of fibers. Only *L. ferruginea, L. fruticosa,* and *L. squamulosa* are known to spread vegetatively by underground rhizomes.

The morphological diversity of this group has been underestimated in the past because of the incomplete knowledge of most of the Caribbean taxa. For example, the group is often said to lack spurs, but many Cuban species (e.g., *L. macrophylla, L. ekmanii, L. obtusa, L. nipensis*) have at least small spurs near the apex of the filament. The species of this group are said to bear their flowers in fascicles, but *L. heptamera* and *L. buchii* often have short racemes. Other peculiarities of the group and the relationships between its many species are discussed in detail below.

Sections PIERIDOPSIS, ARSENOCOCCUS, and MARIA all differ from sect. LYONIA in lacking ferrugineous, peltate scales and in having leaves with the epidermal cells only very occasionally lignified and only rarely with a hypodermis, and petiolar vascular tissue that does not consistently form a cylinder. In addition, species in these sections usually have long, unicellular hairs on their staminal filaments (vs. merely roughened filaments) and thickened sutures that only occasionally separate as a unit from the adjacent valves in dehiscence; they usually spread vegetatively by horizontal underground rhizomes. These three sections are probably more closely related to each other than to sect. LYONIA (see also Judd, 1979). Sections ARSENOCOCCUS and PIERIDOPSIS are especially close since both have an indumentum of characteristic long-headed, multicellular hairs (vs. short-headed hairs in sect. MARIA), but sect. MARIA is quite similar to some species of sect. PIERIDOPSIS in corolla and capsule shape, filament and spur morphology, and placenta position. Section PIERIDOPSIS tends to connect sects. ARSENOCOCCUS and MARIA, which would otherwise appear very distinctive. One could make a case for placing these three sections in one subgenus; a second subgenus would contain only species placed in sect. LYONIA (see Wood, 1961). This has not been done here since the only absolutely constant character distinguishing the two groups is the presence of peltate scales in *Lyonia* sect. LYONIA and their absence in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS. The sectional limits accepted here are thus the same as those of Rehder (1924) and Stevens (1969).

The various generic and infrageneric classifications of the species here considered in *Lyonia* are summarized in TABLE 1 (see also Judd, 1979).

TABLE 1. **Comparative treatment of Lyonia by various authors.**

AUTHORS	TAXA			
	Lyonia sect. **Arsenococcus**	**Lyonia** sect. **Pieridopsis**	**Lyonia** sect. **Maria**	**Lyonia** sect. **Lyonia**
Linnaeus (1753)	*Vaccinium*	—	*Andromeda*	—
Michaux (1803) Pursh (1814) Elliott (1817)	*Andromeda*	—	*Andromeda*	*Andromeda*
Nuttall (1818)	*Lyonia*	—	*Andromeda*	*Lyonia*
D. Don (1834)	*Lyonia*	*Pieris*	*Lyonia*	*Lyonia*
De Candolle (1839)	*Lyonia*	*Pieris* sect. 1	*Leucothoë* sects. *Maria*, *Euleucothoë*	*Lyonia*
Bentham & Hooker (1876)	*Lyonia* sect. 2	*Pieris* sect. *Eupieris*	*Pieris* sect. *Maria*	*Lyonia* sect. 1
Gray (1878)	*Andromeda* subg. *Lyonia*	*Andromeda* subg. *Pieris* (Asiatic subsect.)	*Andromeda* subg. *Pieris* subsect. *Maria*	*Andromeda* subg. *Lyonia*
Britton & Brown (1913)	*Xolisma*	—	*Neopieris*	*Xolisma*
Small (1914)	*Arsenococcus*	—	*Neopieris* / *Desmothamnus*	*Xolisma*
Rehder (1924, 1927)	*Xolisma* sect. *Arsenococcus*	*Xolisma* sect. *Pieridopsis*	*Xolisma* sect. *Maria*	*Xolisma* sect. *Lyonia*
Wood (1961)	*Lyonia* sect. *Maria*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Maria*	*Lyonia* sect. *Lyonia*

PHYLOGENETIC ANALYSIS

Lyonia sect. LYONIA includes 27 species (34 taxa) and is very diverse in the Greater Antilles. The phylogenetic relationships in this section were investigated using the method of Wagner (1961, 1962, 1969). Thirty-two characters were used and assigned generalized and specialized states; TABLE 2 lists these characters. All taxa recognized were considered to be "Operational Taxonomic Units" (OTUs). For each of the characters, each OTU was scored 0 if generalized and 1 if specialized. When both generalized and specialized states of any given character were present in an OTU, that character was scored as "var." (variable) but was also scored as either 0 or 1, depending upon which was more common within—or characteristic of—that OTU. When two or more states of a given character are considered derived, each is given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). All of the OTUs are listed in TABLE 3, together with the character divergence values for each. The total divergence index of each taxon was determined by adding the individual divergence values of each character. Then mutual groupings of derived character states between taxa were determined, and the taxa were arranged according to these groupings. They were then plotted on a concentric

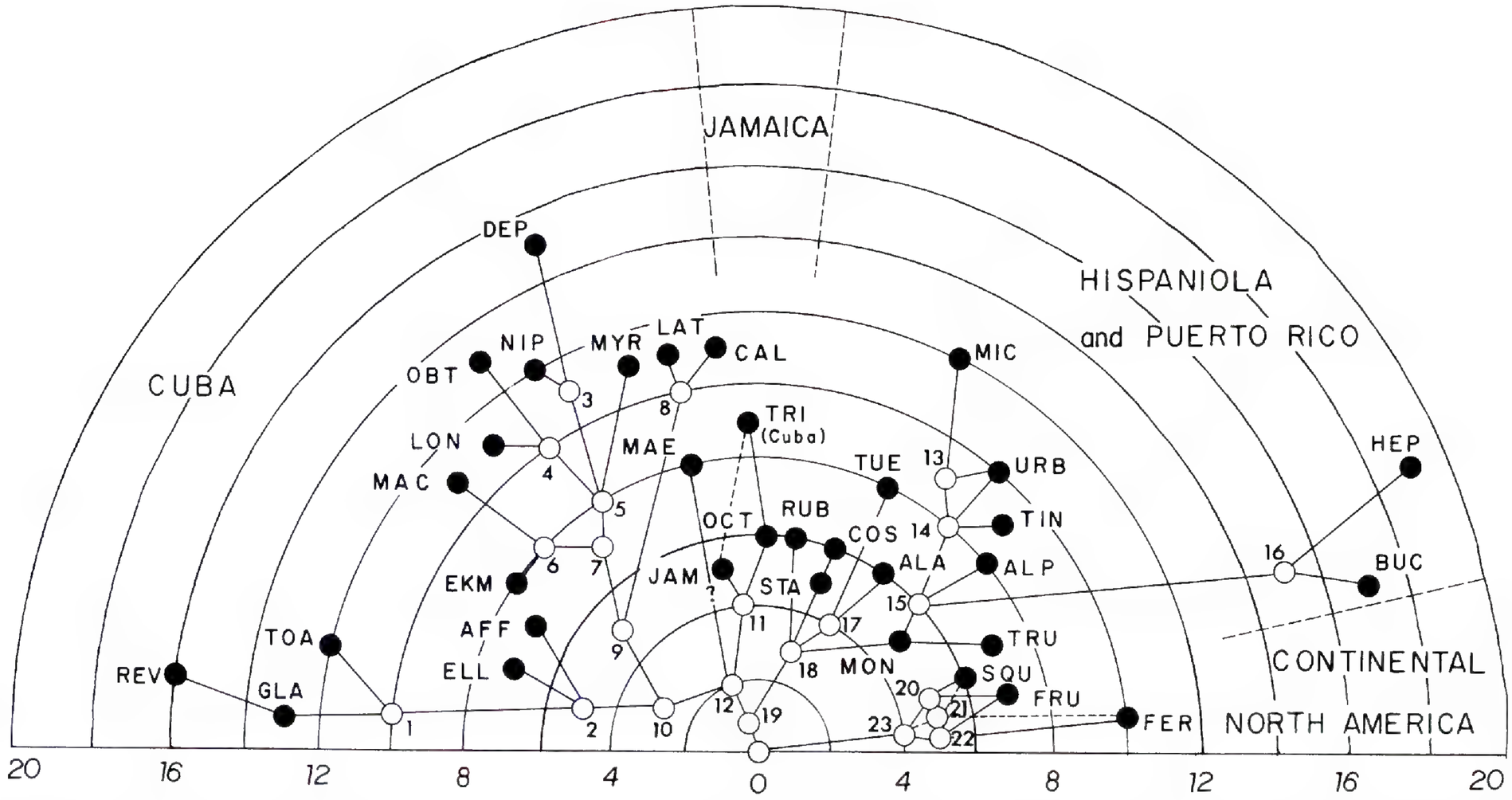


FIGURE 1. Wagner Tree for species and varieties of *Lyonia* sect. LYONIA: present-day taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles).

graph (FIGURE 1), the radii being determined by the mutual groupings of characters, and the distance from the center by the divergence of each OTU. Thus, only the branching points and the evolutionary divergence values (i.e., the length of the lines) indicated by this figure are meaningful.

As previously discussed (see Judd, 1979), the Wagner method requires that numerous assumptions be made regarding the derived and the generalized state of each character. These assumptions are often rather subjective and introduce a major source of both error and circular reasoning.

Characters in which the derived state could be determined by functional and/or ecological considerations (in conjunction with out-group comparison) include: B, C, G, I, M, N, S, T, Y, Z, AA, CC, and HH (TABLE 2). The dense covering of unicellular hairs on the abaxial leaf surface (G) of many species may be an adaptation to reduce water loss; species lacking this adaptation tend to grow in more mesic environments (such as cloud forests or moist montane forests), while taxa with it often grow in dryer oak-pine or pine savannas or thickets, although many exceptions occur. Similarly, taxa with strongly revolute leaves (I) tend to grow in extreme environments. Thus *Lyonia glandulosa* and *L. nipensis* var. *depressinerva* are found on the limonite plateau near Moa, Cuba. In such environments, taxa from many different families have convergently evolved this leaf morphology, and even within the Andromedeae such small and strongly revolute leaves are found in *Tepuia* Camp and in several Brazilian species of *Agarista* that grow in similar stressful habitats. Plants with rigidly ascending branches bearing reduced leaves (C) occur only in species adapted to very sunny and seasonally very dry habitats (i.e., usually savannas or open pine forests). This condition is possibly photosynthetically adaptive and is useful in reducing water loss or overheating due to solar radiation (Horn, 1975; Gates, 1968). Some species such as *L. urbaniana, L. microcarpa,* and *L. alpina* characteristically have a dense covering of long-stalked, ferrugineous scales (M, N) on their leaves, and the first two have their stomata sunken into pockets formed in the lower leaf surface by the densely raised-reticulate (S) veins. These species also always have a dense layer of unicellular hairs on their abaxial leaf surfaces. This complex of characters usually occurs in taxa growing in rather high elevations and is probably of adaptive significance. Such high-elevation species are also often densely branched shrubs with fairly small leaves. The presence of strongly depressed leaf veins (T) is characteristic of many taxa of stressful environments (i.e., dry, sterile sands or lateritic soils over serpentine) and may affect the physiological functioning of the leaf. The presence of 7-, 6-, (or 4-)merous flowers (Y) is possibly due to selection for larger (or smaller) flowers; unfortunately, the pollination biology of the Caribbean species has not been well studied. The shape and pubescence of the corolla (Z, AA) and the presence of filament spurs (CC) may also be related to the pollination biology of the species. The presence of spurs in many of the Cuban species was considered to be a generalized condition because the spurs are morphologically identical to those present in many species of sects. PIERIDOPSIS, MARIA, and ARSENOCOCCUS. Spurs have been lost independently in several Asian and the majority of West Indian species. Finally, some species of higher elevations

TABLE 2. **Characters used in phylogenetic study* of Lyonia sect. Lyonia.**

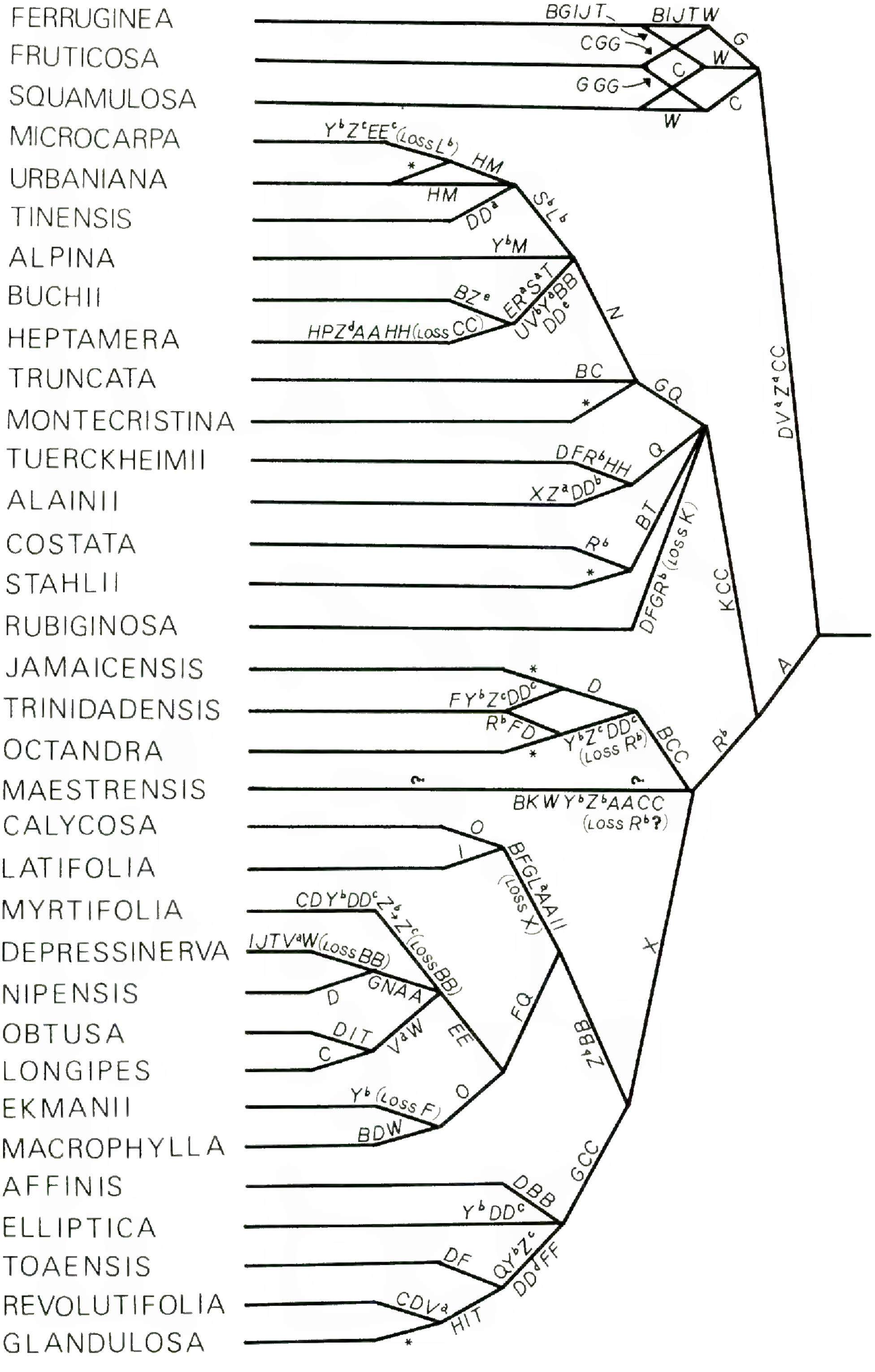
CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Plants producing rhizomes	Yes	No
B	Habit	Moderate-sized to small shrubs	Sometimes large trees
C	Ultimate branchlets	Not rigidly ascending; leaves not reduced near tips	At least sometimes rigidly ascending; leaves reduced in size
D	Stem pubescence (unicellular hairs)	Lacking hairs to moderately covered with them	At least sometimes densely pubescent
E	Presence of short, unicellular hairs on midvein of adaxial leaf surface	Yes	No
F	Short, unicellular hairs on midvein of abaxial surface of leaves	Lacking	Often present (at least at base)
G	Abaxial leaf surface with a dense layer of unicellular hairs	No	Yes
H	Texture of adaxial leaf surface	± Smooth	At least sometimes roughened (persistent bases of peltate scales)
I	Leaf margin strongly revolute	No	Yes
J	Peltate scales (abaxial leaf surface)	± One type	Two distinct morphological types
K	Marginal dentation of leaf	± Entire to obscurely toothed	Often strongly and irregularly toothed
L	Color of peltate scales (on leaves)	Rusty, reddish	a. ± Golden b. Light to dark brown
M	Density of peltate scales on leaf surfaces	Sparse to moderate	Often dense

TABLE 2 (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
N	Stalks of peltate scales ± sunken into abaxial leaf epidermis	Yes	No
O	Length of petiole	Short to moderate	Often elongated (> 10 mm.)
P	Leaf base	Cuneate to rounded or attenuate	Cordate
Q	Leaf apex	At least sometimes acuminate	Acute, obtuse, rounded, or truncate
R	Distribution of unicellular hairs on petiole	Limited to adaxial surface	a. Completely lacking b. Often or sometimes covering all surfaces
S	Venation of leaves (abaxial surface)	Veins ± obscure to laxly reticulate; lacunae lacking	a. Veins coarsely raised-reticulate; lacunae present b. Veins finely raised-reticulate; lacunae present
T	2° veins on adaxial leaf surface usually depressed	No	Yes
U	Petiole anatomy	Medullary bundles lacking	Several medullary bundles present
V	2° and 3° veins of leaf (as seen in cross section)	Transcurrent	a. Semitranscurrent b. Embedded
W	Leaf hypodermis	Strongly to at least partially developed	Lacking
X	Epidermal lignification of leaves	Cells ± uniformly lignified	Cells with inner periclinal walls strongly thickened and lignified
Y	Number of flower parts	5 per whorl	a. 6 or 7 per whorl b. 4 per whorl

Z	Size and shape of corolla	Medium sized, ± cylindrical	a. Shortly urceolate to globose b. Elongate-urceolate c. Minute and ± cylindrical or slightly urceolate d. Large (> 7 mm. wide), urceolate e. Large (> 7 mm. wide), campanulate
AA	Density of peltate scales on corolla	± Sparse	± Dense
BB	Length of calyx lobes	Short (< 2 mm.)	Long (often 3–4 mm.)
CC	Filament spurs	± Well developed	Lacking or minute
DD	Shape of capsules	Ovoid to ellipsoid	a. Urn shaped b. ± Subglobose c. Narrowly ovoid d. Minute, extremely narrowly ovoid or ellipsoid e. Very large, subglobose to short-ovoid
EE	Pedicels elongated in fruit	No	Yes
FF	Flower articulated with pedicel	Yes	No
GG	Capsules often with thickened ridge (resembling suture) running down center of each valve	No	Yes
HH	Twigs (thickness)	Usually ± slender	Very stout
II	Calyx lobes densely covered with peltate scales on adaxial surface	No	Yes

*Wagner Method.


FERRUGINEA
FRUTICOSA
SQUAMULOSA
MICROCARPA
URBANIANA
TINENSIS
ALPINA
BUCHII
HEPTAMERA
TRUNCATA
MONTECRISTINA
TUERCKHEIMII
ALAINII
COSTATA
STAHLII
RUBIGINOSA
JAMAICENSIS
TRINIDADENSIS
OCTANDRA
MAESTRENSIS
CALYCOSA
LATIFOLIA
MYRTIFOLIA
DEPRESSINERVA
NIPENSIS
OBTUSA
LONGIPES
EKMANII
MACROPHYLLA
AFFINIS
ELLIPTICA
TOAENSIS
REVOLUTIFOLIA
GLANDULOSA
BGIJT
BIJTW
CGG
G
W
C
GGG
C
W
YbZcEEc (LOSS Lb)
HM
*
HM
DDa
SdLd
YbM
BZe
ERaSaT
UVbYaBB
DDe
HPZdAAHH (LOSS CC)
N
BC
GQ
*
DFRbHH
Q
XZaDDb
BT
Rb
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DFGRb (LOSS K)
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A
DVaZaCC
Rb
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FYbZcDDc
D
RbFD
YbZcDDc (LOSS Rb)
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CDYbDDc
Zb, Zc (LOSS BB)
IJTVaW (LOSS BB)
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BBaZ
YbDDc
YbDDc (LOSS F)
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BDW
GCC
DBB
YbDDc
DF
QYbZc
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CDVa
HIT
*

(such as *L. tuerckheimii* or *L. heptamera*) have stouter twigs (HH) and are shorter shrubs (B) than their relatives at lower altitudes. These characteristics have evolved independently in several evolutionary lines in response to the similar climatic factors facing plants of high elevations.

The derived states of many characters (A, B, E, F, H, L, M, N, O, P, R, S, U, V, W, Z, AA, BB, DD, EE, FF, GG, HH, II) were chosen, at least in part, because the condition was unusual within *Lyonia* sect. LYONIA (in-group comparison). It is admitted that the criterion of "uncommonness" cannot be defended, since the distribution of character states depends upon the phylogeny of the group and on where within this sequence a particular character changes (Stevens, 1980). Thus, this criterion was often used in conjunction with the preceding and/or the following ones. The derived states of the characters A, E, G, H, S, T, U, Y, FF, and GG were chosen, at least in part, because the condition was limited to one section of the genus (out-group comparison). Finally, a few character states (D, H, J, K, O, Q, X) were considered to be derived because they were correlated with other derived character states.

The Wagner tree resulting from the above procedure (FIGURE 1) indicates that the species of *Lyonia* sect. LYONIA belong to three major phyletic groups, with a small fourth group intermediate between two of these. (The derived character states of each OTU are shown in FIGURE 2.) The first is here called the Cuban group because all the taxa within it are native to either Cuba or the Isle of Pines. Only two Cuban species, *L. trinidadensis* and possibly *L. maestrensis,* have their greatest affinities with species of other islands. The Cuban group is composed of three related evolutionary lines, which are for convenience termed the *L. glandulosa* line (GLA), the *L. obtusa–L. nipensis* line (OBT-NIP), and the *L. latifolia* line (LAT). The second major evolutionary group is called the Hispaniolan group because all the taxa within it are native either to Hispaniola or to the adjacent islands of Puerto Rico and St. Thomas. It is composed of two subgroups, the *L. tuerckheimii* "line" (TUE), and the *L. microcarpa–L. truncata–L. heptamera* line (MIC-TRU-HEP). *Lyonia jamaicensis* and *L. octandra,* both native to Jamaica, along with *L. trinidadensis,* endemic to Las Villas Province, Cuba, form a small group of species intermediate between the larger Cuban and Hispaniolan species groups. The position of *L. maestrensis* is in doubt because mature capsules and flowers of this species have not been seen. It may be related to *L. latifolia,* since it appears, from the material now available, to have similarly shaped, densely lepidote corollas. However, it has distinctly toothed leaves, which may indicate a relationship with some of the more generalized species of the Hispaniolan group. The third major phylogenetic

FIGURE 2. Phylogenetic diagram for species and varieties of *Lyonia* sect. LYONIA showing derived characteristics of each taxon and evolutionary line. Newly acquired derived character states shown for each branching point (length of lines has no evolutionary meaning). Each taxon placed at end of line because extant species probably not directly ancestral to any others.

group has only three species (*L. ferruginea*, *L. fruticosa*, and *L. squamulosa*) and is limited to continental North America. It is called the North American group.

The species of the North American group all have stems at least sometimes densely pubescent (D), fibers surrounding the leaf veins usually not forming girders between the adaxial and abaxial leaf epidermis (V^a), and shortly urceolate corollas (Z^a); all lack prominent spurs on their filaments (CC) (FIGURE 2). The group is especially distinctive in its ability to spread vegetatively by horizontal underground rhizomes, which arise from large, woody, elongated burls, and in its characteristic shortly urceolate flowers. No other species of sect. LYONIA spreads vegetatively, and only *Lyonia alainii* has similarly shaped corollas.

Nearly all the Cuban taxa have petioles at least sometimes densely pubescent on all surfaces (R^b) and leaves in which the inner periclinal walls of the epidermal cells are especially strongly thickened and lignified (X). Within this group, *Lyonia affinis* and *L. elliptica* are the least specialized, but even these taxa are advanced in their lack of filament spurs (CC) and in the dense layer of unicellular hairs covering their abaxial leaf surfaces (G).

The *Lyonia glandulosa* evolutionary line in Cuba has developed the added specializations of leaf apices never acuminate (Q), 4-merous flowers (Y^b) with extremely small corollas (Z^c), and extremely narrowly ovoid to ellipsoid capsules (DD^b) lacking a visible articulation (FF) with the pedicel. The most advanced taxon of this phylogenetic group, *L. glandulosa* var. *revolutifolia*, also has strongly revolute leaves (I) with depressed veins (T). The above-mentioned characters make *L. toaënsis* and *L. glandulosa* among the more easily recognized of the Cuban species.

Most of the taxa of the *Lyonia obtusa–L. nipensis* evolutionary line are characterized by petioles often with unicellular hairs on all surfaces (R^b); leaves without acuminate apices (Q) but with epidermal cells having prominently thickened and lignified inner periclinal walls (X), and with short, unicellular hairs often present on the midvein of the lower surface (F); elongate-urceolate corollas (Z^b); and often elongated calyx lobes (BB). Within this group, *L. ekmanii* and *L. macrophylla* are probably closely related, and both characteristically have leaves with elongated petioles (O). It is interesting that the leaves of *L. macrophylla* lack a hypodermis, while those of *L. ekmanii* have one. *Lyonia macrophylla* also differs from *L. ekmanii* in its more consistently 5-merous capsules and its more densely pubescent twigs. The remaining taxa of the *L. obtusa–L. nipensis* line all have the pedicel of the fruit at least sometimes elongated (EE). Among these taxa, *L. myrtilloides* is rather isolated and is distinguished by often rigidly ascending branches bearing very small leaves (C), more or less densely pubescent stems (D), 4-merous flowers (Y^b), very small corollas (Z^c), and narrowly ovoid capsules (DD^c). *Lyonia nipensis* is distinguished by additional derived character states: abaxial leaf surface with a dense covering of unicellular hairs (G), stalks of peltate scales not sunken into abaxial epidermis (N), and densely lepidote corollas (AA). *Lyonia nipensis* var. *depressinerva* has several distinctive vegetative modifications, such as two types of peltate scales (J), and strongly

revolute leaves (I) with depressed veins (T) and various anatomical pecularities (W, V^a). *Lyonia obtusa* is characterized by the lack of a hypodermis (W) and by the lignified sheaths of its leaf veins (V^a). *Lyonia obtusa* var. *obtusa* sometimes has strongly revolute leaves with clearly depressed major veins. There are several examples of parallel evolution of characters between these two species, which are evidently very closely related.

The *Lyonia latifolia* phylogenetic line, which is very distinctive (especially in floral morphology), is probably an offshoot from extinct primitive members of the Cuban group. *Lyonia latifolia* vars. *latifolia* and *calycosa* are distinguished by the following additional derived character states: sometimes arborescent habit (B); leaves with a dense covering of unicellular hairs on the abaxial surface (G), with short, unicellular hairs at least sometimes present on the midvein of the abaxial surface (F), and golden-colored, peltate scales (L^a); elongated calyx lobes with the adaxial surface densely covered by peltate scales (II); and elongate-urceolate (Z^b), densely lepidote (AA) corollas. *Lyonia latifolia* has uniformly lignified epidermal cells, an unusual characteristic among Cuban species.

With respect to the two remaining species that are endemic to Cuba, the relationships of *Lyonia maestrensis* are essentially unknown, while *L. trinidadensis* is undoubtedly more closely related to the Jamaican *L. octandra* and *L. jamaicensis* than it is to any other Cuban species. These three species form a small, rather nondescript group intermediate between the Cuban and Hispaniolan groups. They are characterized by their arborescent habit (B), petioles often covered on all surfaces with unicellular hairs (R^b) (lost in *L. octandra*), and filaments without well-developed spurs (CC). *Lyonia octandra* and *L. trinidadensis* have the additional specializations of small (Z^c), 4-merous (Y^b) flowers and narrowly ovoid capsules (DD^c).

Nearly all the species of Hispaniola and Puerto Rico are characterized by having at least sometimes strongly toothed leaves (B) and by lacking well-developed filament spurs (CC). The *Lyonia tuerckheimii* group includes a rather generalized assortment of taxa united more by their primitive traits than by any shared derived characters. All taxa lack unicellular hairs on the abaxial leaf surface (except some plants of *L. rubiginosa* var. *rubiginosa*), have obscure to laxly reticulate leaf veins, and are more or less sparsely to moderately lepidote. Several taxa at least occasionally have acuminate-tipped leaves. It is interesting that three of the five taxa comprising this group (*L. rubiginosa* vars. *costata* and *stahlii*, and *L. alainii*) often occur in cloud forests. The more generalized taxa within the group (e.g., *L. rubiginosa*) grow at low altitudes, while the more specialized *L. tuerckheimii* has become adapted to high-elevation pine forests. *Lyonia tuerckheimii* is distinctive in having densely pubescent (D), stout (HH) twigs; short, unicellular hairs on the midvein of the abaxial leaf surface (F); petioles at least sometimes with unicellular hairs on all sides (R^b); rigidly coriaceous leaves; and a rounded, "compact" habit.

The species of the *Lyonia microcarpa–L. truncata–L. heptamera* evolutionary line are all distinguished by the following additional derived characters: leaves not acuminate tipped (Q) but with a dense layer of unicellular hairs

on the abaxial surface (G). The more generalized taxa, such as *L. truncata* vars. *montecristina* and *truncata,* occur at lower elevations than the more advanced ones (*L. alpina, L. tinensis, L. urbaniana, L. microcarpa,* and *L. heptamera*). *Lyonia tinensis, L. microcarpa,* and *L. urbaniana* are distinctive in that their leaves have a densely and finely raised-reticulate network of veins on the lower surface (S^b). The stomata of these species are present chiefly in the cavities formed in the abaxial surface by the raised-reticulate veins, and the stalks of their peltate scales are not sunken into the leaf epidermis (N). *Lyonia microcarpa* and *L. urbaniana* also have densely lepidote (M), very small leaves. *Lyonia buchii* and *L. heptamera* probably evolved from an extinct and generalized taxon of this phylogenetic line. They are extremely specialized, are thus distinctive in both floral and vegetative characters, and form a distinctive evolutionary grade. They have petioles lacking unicellular hairs (R^a) and with medullary bundles within the xylem cylinder (U); leaf veins with a distinctive lignified sheath (V^b), very strongly and coarsely raised and reticulate on the abaxial surface (S^a), slightly depressed on the adaxial (T); 6- or 7-merous flowers (Y^a); elongated calyx lobes (BB); and very large, subglobose to shortly ovoid capsules (DD^c). *Lyonia heptamera* is the only Hispaniolan species that sometimes has well-developed spurs on its filaments, and *L. buchii* is unique in its very widely urceolate to campanulate corollas.

Many examples of parallel evolution can be found among the various phylogenetic groups discussed above. These can be determined from FIGURE 2 and TABLE 3. One of the most interesting is the loss of filament spurs by most of the species of sect. LYONIA. Others are the development of an arborescent habit; densely pubescent stems; small leaves; abaxial leaf surface densely covered with unicellular hairs (note: the presence or absence of these hairs seems to be quite inconstant in a few generalized species), or with peltate scales with stalks not impressed into the epidermis; adaxial leaf surface roughened and with depressed secondary veins; leaf margin strongly revolute; the loss of a leaf hypodermis; 4-merous flowers with small corollas; and narrowly ovoid, 4-merous capsules.

The three major phyletic groups and their various subgroups are not given formal taxonomic recognition because of the small phenetic distance between the extant generalized species (e.g., *Lyonia affinis, L. ekmanii, L. jamaicensis, L. rubiginosa, L. truncata*).

Finally, one should not try to judge specific limits from FIGURES 1 and 2 because the frequency of individuals intermediate between any two OTUs and the nature of the characters separating them were not taken into account. For example, *Lyonia nipensis* var. *nipensis* and *L. nipensis* var. *depressinerva* appear to be widely separated in number of derived characters, while *L. tinensis* and *L. urbaniana* appear to be very similar. It is true that the extreme forms of the two varieties of *L. nipensis* appear more different than do *L. urbaniana* and *L. tinensis,* but there is a consistent morphological gap in the complex of characters defining the latter two species, while the characters distinguishing the varieties of *L. nipensis* are extremely variable, with more or less intermediate plants existing. In addition, the varieties of *L. nipensis*

differ only in vegetative characters that are frequently rather variable within related species, while *L. tinensis* and *L. urbaniana* differ not only vegetatively but also in several flower and fruit characters.

EVOLUTION AND DISTRIBUTION

The 35 species of *Lyonia* recognized here are divided into four sections. Section PIERIDOPSIS, comprising five species, occurs in eastern Asia in an arc from northern Pakistan to Japan, and south to the Malay Peninsula. The greatest diversity of the genus, although not the greatest number of species, is in eastern North America, where three sections are represented. Section ARSENOCOCCUS, including the single species *L. ligustrina,* is found only in the eastern United States, in the Coastal Plain, Piedmont, and Appalachian and Ozark mountains. Section MARIA, comprising *L. mariana* and *L. lucida,* occurs in the Coastal Plain of eastern North America. *Lyonia lucida* is also native to Cuba (Pinar del Río and the Isle of Pines). Section LYONIA is the largest subgroup in the genus, containing 27 species. All of these except *L. ferruginea* and *L. fruticosa* (of the southeastern United States) and *L. squamulosa* (of the mountains of eastern and southern Mexico) are native to the Greater Antilles, occurring mostly in the mountains.

Lyonia is an ancient genus and was probably widely distributed in the mesophytic forests that once extended around the globe in northern regions. The characteristic assemblage of taxa in these forests has often been called the Arcto-tertiary Geoflora (Chaney, 1947). However, Wolfe (1969, 1975) has suggested that the concept of a geoflora is faulty. In 1969 he wrote, "it is extremely improbable from the genetic and physiological viewpoint that many lineages could have remained in association throughout the Tertiary." This may well be true but does not alter the fact that the antiquity of *Lyonia* is illustrated by its Tertiary relict disjunction pattern between eastern North America and eastern Asia, a distribution pattern first brought to the attention of American and European scientists by Asa Gray (Wood, 1972). This disjunction is made even more obvious when the phylogenetic relationships within *Lyonia* are considered. *Lyonia ligustrina* (sect. ARSENOCOCCUS) is probably more closely related to the Asian species (sect. PIERIDOPSIS) than it is to any other species of North America or the Caribbean region. However, sect. MARIA is also phyletically closer to the Asian species than it is to the West Indian species of the genus (sect. LYONIA). Many other genera show disjunction patterns similar to that shown by the group *Lyonia* sects. ARSENOCOCCUS, MARIA, and PIERIDOPSIS, and within the Ericaceae some examples are *Elliottia* (Bohm *et al.,* 1978), *Pieris* (Judd, 1981), *Epigaea, Menziesia, Leucothoë,* and various sections of *Gaultheria* and *Rhododendron* (Li, 1952; Wood, 1972). Paleobotanical findings have shown that genera, especially the woody ones, showing this pattern once occurred over wide areas from which they are now missing. The extant representatives of these genera are descendents of the survivors of the gradual climatic deterioration, volcanism, orogenic activity, and glaciation that have occurred since the mid-Tertiary (Li, 1952).

TABLE 3. **Character divergence values for each taxon used to construct Wagner Tree.***

CHARACTER	TAXA																																		
	GLA	REV	TOA	LAT	CAL	MAE	AFF	MAC	EKM	OBT	LON	NIP	DEP	MYR	TRI	OCT	JAM	RUB	STA	ELL	COS	ALA	TUE	TRU	MON	TIN	URB	MIC	ALP	BUC	HEP	SQU	FER	FRU
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
B	0	0	0	1	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0
C	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1
D	0	1	1	0	0	0	1	1	0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
F	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
G	1	1	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1
H	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
I	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
J	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
K	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
L	0	0	0	1A	1A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	0	0	0	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
N	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0
O	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Q	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0
R	1B	1B	1B	1B	1B	0	1B	1B	1B	1B	1B	1B	1B	1B	1B	0	1B	1B	0	1B	1B	0	1B	0	0	0	0	0	0	1A	1A	0	0	0	0
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	1B	0	1A	1A	0	0	0	0

	GLA	REV	TOA	LAT	CAL	MAE	AFF	MAC	EKM	OBT	LON	NIP	DEP	MYR	TRI	OCT	JAM	RUB	STA	ELL	COS	ALA	TUE	TRU	MON	TIN	URB	MIC	ALP	BUC	HEP	SQU	FER	FRU
T	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
V	0	1A	0	0	0	0	0	0	0	1A	1A	0	1A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1B	1B	1A	1A	1A
W	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
X	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Y	1B	1B	1B	0	0	1B	0	0	1B	0	0	0	0	1B	1B	1B	0	0	0	1B	0	0	0	0	0	0	0	1B	1B	1A	1A	0	0	0
Z	1C	1C	1C	1B	1B	1B	0	1B	1B	1B	1B	1B	1B	1C	1C	1C	0	0	0	0	0	1A	0	0	0	0	0	1C	0	1E	1D	1A	1A	1A
AA	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
BB	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
CC	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
DD	1D	1D	1D	0	0	0	0	0	0	0	0	0	0	1C	1C	1C	0	0	0	1C	0	1B	0	0	0	1A	0	1C	0	1E	1E	0	0	0
EE	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FF	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
HH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
II	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL	13	16	12	11	11	8	7	11	8	13	11	12	15	11	9	6	5	6	5	7	6	7	8	7	5	9	10	12	8	17	19	6	10	7

*Each taxon is abbreviated by the first three letters of its name.

The species of *Lyonia* sect. LYONIA show disjunction patterns between the southeastern U. S. Coastal Plain, the montane areas of eastern and southern Mexico, and the islands of the Greater Antilles. There are many similarities between the deciduous forest formations of the eastern United States and the montane temperate forests of Mexico. Several species show disjunct distributions in these two areas, and a number of species pairs have representatives in the two regions (see Miranda & Sharp, 1950; Dressler, 1954; Martin & Harrell, 1957; Graham, 1964, 1973; Rzedowski, 1965; Gómez-Pompa, 1973). This eastern North American–Mexican relationship is illustrated by *L. ferruginea* and *L. fruticosa,* which occur on the Coastal Plain of South Carolina, Georgia, and Florida, and which are extremely closely related to *L. squamulosa,* of the Sierra Madre Oriental of Mexico. These three taxa are more closely related to each other than to any of the species of this section in the Greater Antilles.

Some authorities (e.g., Dressler, 1954) believe that the Mexican–eastern North American species migrated to Mexico during periods of ice advance; others (e.g., Braun, 1955; Martin & Harrell, 1957) contend that temperate plants reached Mexico at least by the middle of the Cenozoic. Recent palynological studies on Cenozoic deposits in Veracruz reveal a distinct and diverse arborescent temperate community already present in eastern Mexico by middle Miocene times, and collective data on the history of temperate trees and shrubs throughout northern Latin America demonstrate progressive independent southward migration of these elements (Graham, 1972, 1973). Thus, the floristic relationships between the eastern United States and eastern Mexico (and between *Lyonia ferruginea, L. fruticosa,* and *L. squamulosa*) may have had their origin in Tertiary rather than Pleistocene time.

Before the relationships of the Caribbean taxa are discussed, the geology and palynology of this area should be outlined briefly. Although numerous land bridges have been postulated between either Central or North America and the West Indies, these areas were probably never connected (MacGillavry, 1970; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972; Graham, 1972). During the Early Cretaceous, probably only a few volcanic peaks were emergent in the Caribbean (Graham, 1972), and until the end of the Cretaceous, numerous small islands continued to characterize the region (MacGillavry, 1970; Graham, 1972; Malfait & Dinkelman, 1972; Graham & Jarzen, 1969). After the late or middle Eocene, western and central Cuba were uplifted and remained an emergent stable platform. Cuba is thus the oldest of the West Indian islands, with Hispaniola and Puerto Rico being younger, and the Lesser Antilles the youngest of all (Malfait & Dinkelman, 1972; Nagel, 1971). By the Oligocene, there was extensive land area within the Caribbean, probably considerably greater than that existing today, and by late Miocene time, the islands of the Greater Antilles had essentially attained their modern aspect (Malfait & Dinkelman, 1972; Graham, 1972; Graham & Jarzen, 1969). It has become apparent from recent palynological studies of the San Sebastian formation of Puerto Rico that the Oligocene vegetation of the island was similar in generic composition to the modern Antillean flora. Among the 44 pollen and spore types found, 31 represent genera now growing in Puerto

Rico (Graham & Jarzen, 1969; Graham, 1972). Graham and Jarzen (1969) have postulated (and there is geologic evidence in support) that the Caribbean land mass of the Oligocene, in addition to being larger than at present (including Hispaniola, Puerto Rico, and the Virgin Islands), was also higher, having reached elevations of 13,000 to 15,000 feet. This would account for the presence in the San Sebastian flora of pollen of *Fagus* L., *Liquidambar* L., and *Nyssa* L., which indicates that an arborescent, cool-temperate community existed. These genera may have migrated into the Oligocene highlands and into the mountains of eastern Mexico at about the same time. There is evidence of the lowering of these highlands through both subsidence and rapid erosion (Graham, 1972; Graham & Jarzen, 1969).

Several genera of Pinar del Río, Cuba, may have reached the Caribbean from the north (i.e., from the southeastern United States). Some of these are *Kalmia* L., *Pieris, Quercus* L. (but see Borhidi & Muñiz, 1971), *Fraxinus* L., and *Pinus* L. (see Howard, 1973, and Alain, 1958). *Lyonia lucida* (sect. MARIA) shows this pattern since it is widespread on the Coastal Plain of

TABLE 4. **Distribution of taxa among the major mountain ranges of Hispaniola.**

I. CORDILLERA CENTRAL–MASSIF DU NORD (8 taxa)

Lyonia rubiginosa var. *costata*
L. tuerckheimii
*L. alainii**
L. truncata var. *montecristina**
*L. tinensis**
*L. urbaniana**
L. buchii
*L. heptamera**

II. MASSIF DE LA SELLE–SIERRA DE BAORUCO (6 taxa)

L. rubiginosa var. *costata*
L. tuerckheimii
L. truncata var. *truncata**
*L. alpina**
*L. microcarpa**
L. buchii

III. SIERRA DE NEIBA (1 taxon)

L. rubiginosa var. *costata*

IV. MASSIF DE LA HOTTE (1 taxon)

L. rubiginosa var. *costata*

V. MASSIF DES CAHOS (1 taxon)

L. buchii

*Taxon endemic to mountain range; see MAP 2.

TABLE 5. **Distribution of taxa among the major mountain ranges of Cuba.**

I. SIERRA DE CRISTAL–SIERRA DE MÍCARA (5 taxa)

Lyonia nipensis var. *nipensis*
L. obtusa var. *longipes**
L. macrophylla
L. glandulosa var. *revolutifolia*
L. latifolia var. *calycosa* (rare)

II. SIERRA MAESTRA (including GRAN PIEDRA) (4 taxa)

*L. affinis**
*L. maestrensis**
L. latifolia var. *latifolia** (Loma del Gato and westward)
L. latifolia var. *calycosa* (Loma del Gato and eastward)

III. SIERRA DE NIPE (3 taxa)

L. nipensis var. *nipensis*
L. macrophylla
L. glandulosa var. *glandulosa**

IV. MOA PLATEAU (3 taxa)

L. nipensis var. *nipensis*
L. macrophylla
L. glandulosa var. *revolutifolia*

V. SIERRA DE MOA–SIERRA DE TOA (4 taxa)

L. nipensis var. *depressinerva**
L. obtusa var. *obtusa*
L. macrophylla
L. glandulosa var. *revolutifolia*

VI. BARACOA REGION (2 taxa)

L. obtusa var. *obtusa*
L. macrophylla

VII. MONTE LIBANON (1 taxon)

L. nipensis var. *nipensis*

VIII. SIERRA DE IMÍAS–ALTO DE IBERIA (1 taxon)

L. latifolia var. *calycosa*

IX. SIERRA DE FRIJOL (PICO GALANO) (1 taxon)

*L. toaënsis**

X. PINAR DEL RÍO–ISLA DE PINOS (3 taxa)

L. lucida
*L. ekmanii**
*L. myrtilloides**

XI. MONTE VERDE–MONTE TORO (1 taxon)

*L. elliptica**

TABLE 5 (*continued*).

XII. SIERRA DE TRINIDAD–SIERRA DE SANCTI SPIRITUS (1 taxon)
*L. trinidadensis**

*Taxon endemic to mountain range; see MAP 1.

the southeastern United States and occurs disjunctly in Pinar del Río and the Isle of Pines.

Lyonia sect. LYONIA is extremely diverse in the West Indies, with twelve species (sixteen taxa) occurring in Cuba, ten (eleven taxa) in Hispaniola, two in Jamaica, one in Puerto Rico, and one in St. Thomas. With the exception of *L. rubiginosa,* all these species are endemic to a single island. *Lyonia rubiginosa* occurs on three islands but has differentiated into three geographically isolated varieties: var. *costata* on Hispaniola, var. *stahlii* on Puerto Rico, and var. *rubiginosa* on St. Thomas.

Within the Greater Antilles, *Lyonia* shows a "Western Continental" distribution pattern (see Asprey & Robbins, 1953; Alain, 1958; Howard, 1973). Genera with this pattern are missing from the Lesser Antilles, are often most diverse in Cuba, and decrease in diversity eastward to the Virgin Islands. Thus, of the thirty Caribbean taxa of *Lyonia,* sixteen are endemic to Cuba, eleven to Hispaniola, two to Jamaica, and one to Puerto Rico. These genera (including *Lyonia*) probably have entered the Caribbean region from the west (i.e., via Mexico and western Cuba). *Lyonia* could not easily have migrated from the north, since an oceanic barrier at least as extensive as the present one separated continental North America and the Greater Antilles in this region during the middle Tertiary (Graham & Jarzen, 1969; Graham, 1972). *Lyonia* was probably dispersed to the topographically diverse Oligocene uplands of the Caribbean by wind because the seeds are small and light and can be blown about. Long-distance dispersal events must be very rare, however, since the great majority of the seeds fall within a short distance of the parental plant (pers. obs.). Once *Lyonia* was established within the Antilles, radiation occurred into diverse habitats, the taxa being primarily isolated by geographic, ecological, and genetic barriers (see below). *Lyonia* possibly spread throughout the Greater Antilles when this region still existed as a single (or two?) large land mass(es), or when the water barriers separating the islands were not as extensive as they are today. The species of Cuba, when compared to those of Puerto Rico, Hispaniola, and the Virgin Islands, are quite distinct, suggesting that Cuba may early have become separate (or perhaps was always distinct) from these islands. *Lyonia rubiginosa* var. *stahlii,* which now exists only on a few of the highest peaks of the Puerto Rican Cordillera Central, and *L. rubiginosa* var. *rubiginosa,* which exists (or once existed) in a population of only a few individuals atop a single peak on St. Thomas, probably are relicts that were more widespread when higher elevations existed on these islands during the Oligocene and Miocene.

As was shown above, within the genus *Lyonia,* the species growing on each island are nearly always most closely related to others on the same island. The generalized species of each island tend to be similar morphologically

and anatomically, and they usually occur in mesic to slightly xeric habitats, such as cloud forests, moist montane forests, or low-elevation pine forests. The advanced species of each of the islands are very distinctive and are usually adapted to various more rigorous habitats, such as thickets on red lateritic soils rich in iron oxide and often developed over serpentine (e.g., *Lyonia glandulosa, L. macrophylla, L. nipensis, L. obtusa, L. truncata* var. *truncata*); sterile, white-sand savannas (e.g., *L. ekmanii, L. myrtilloides*); high-elevation pine forests on igneous soils (e.g., *L. urbaniana, L. heptamera, L. tuerckheimii, L. alpina*); or pine forests or thickets over limestone (some populations of *L. truncata* and *L. microcarpa*).

Lyonia species are rather narrowly endemic and are adapted to specific ecological situations and elevational ranges. Many taxa are found only in single mountain ranges (see TABLES 4 and 5), and a few, such as *L. toaënsis* and *L. rubiginosa* var. *rubiginosa,* are endemic to single peaks. However, on each island a few taxa, such as *L. truncata* and *L. rubiginosa* var. *costata* on Hispaniola, or *L. macrophylla, L. affinis,* and *L. latifolia* on Cuba, are

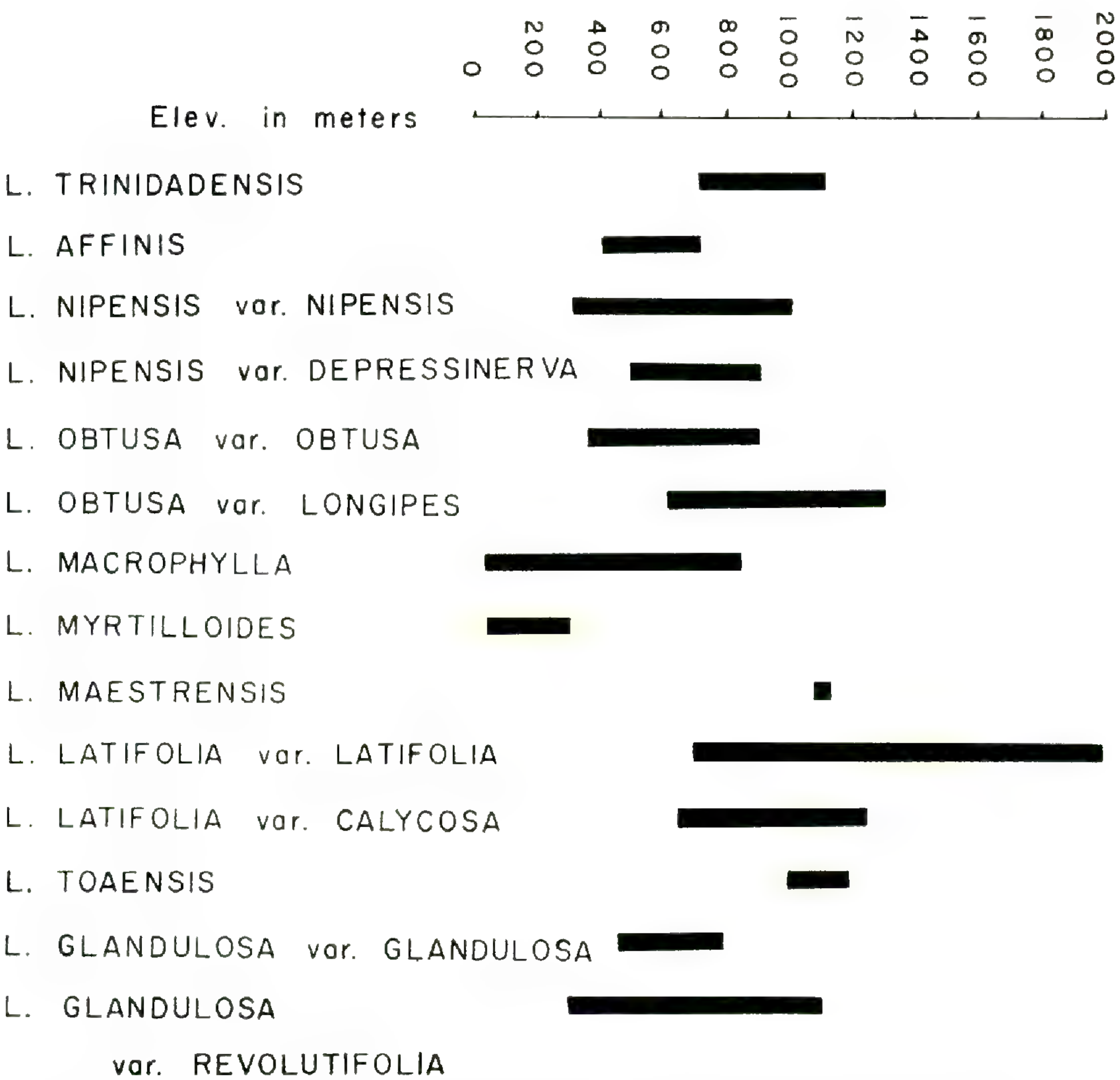


FIGURE 3. Altitudinal ranges of species and varieties of *Lyonia* sect. LYONIA in Cuba (*L. elliptica* and *L. ekmanii* not plotted because of insufficient data).

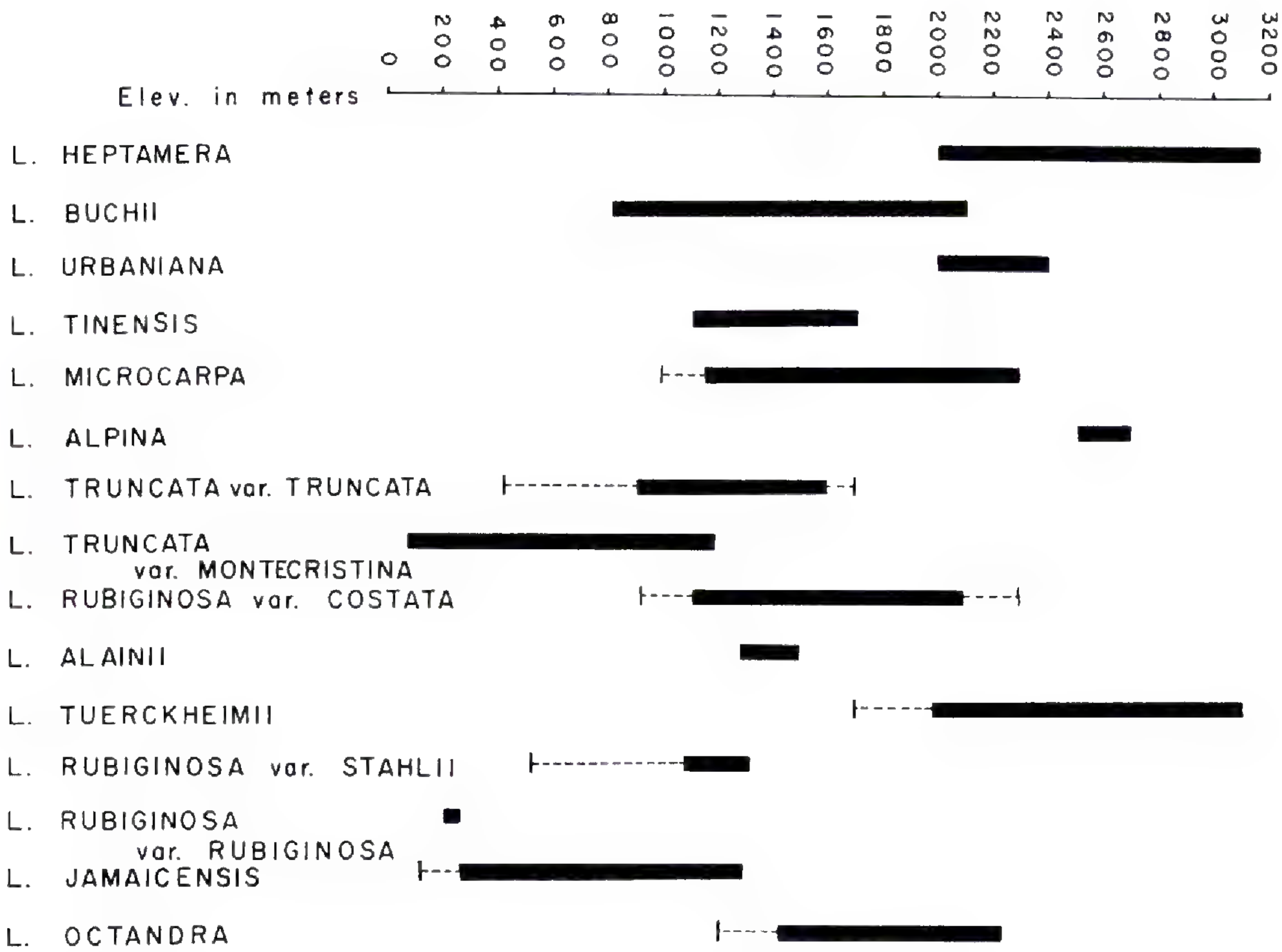
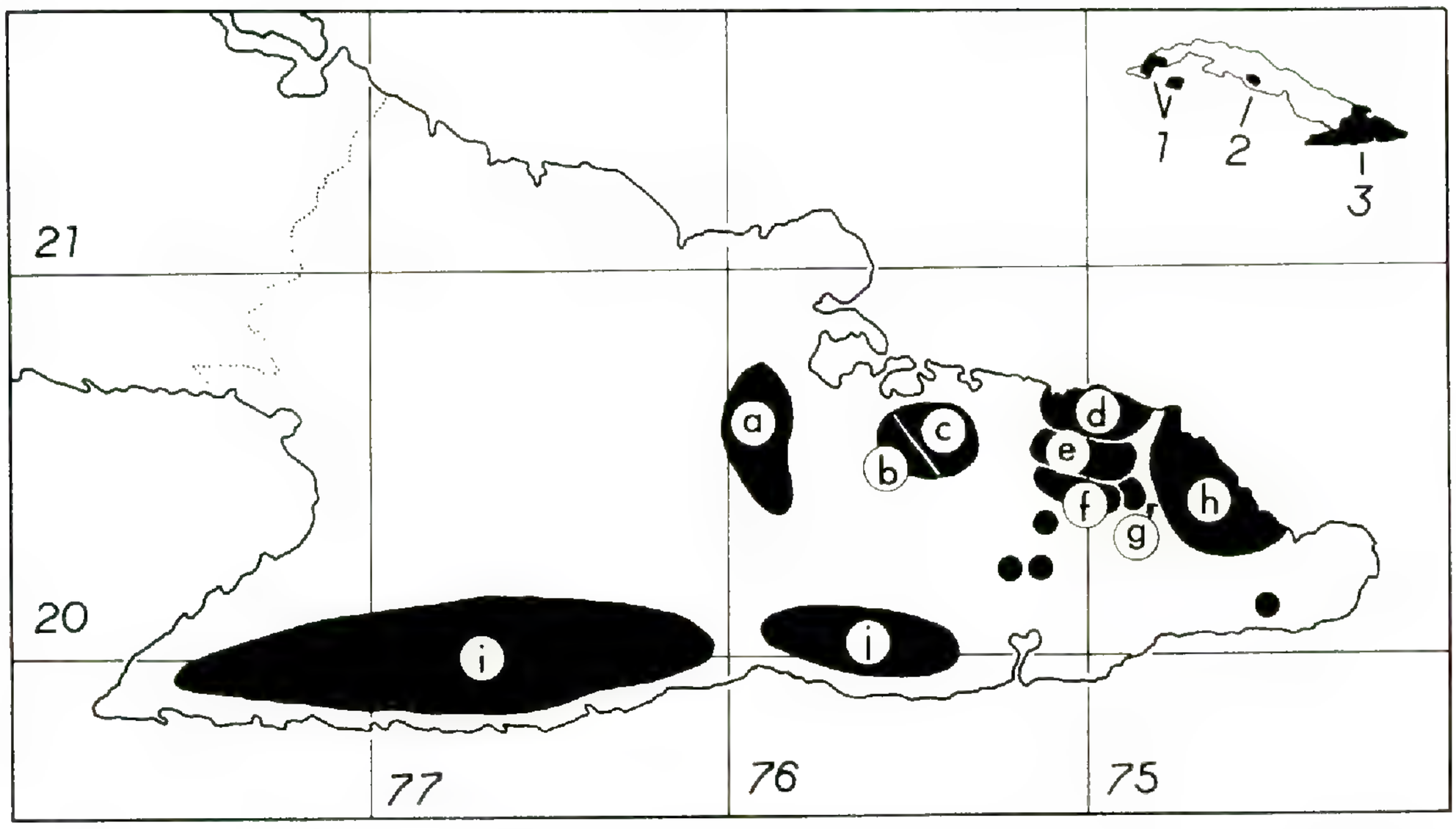


FIGURE 4. Altitudinal ranges of species and varieties of *Lyonia* sect. LYONIA in Hispaniola, Puerto Rico, St. Thomas, and Jamaica.

widespread. These species are often composed of many distinct, somewhat different populations that have sometimes been recognized by earlier botanists as separate species. The most extensive adaptive radiation has occurred in Cuba and Hispaniola, the Caribbean islands with the greatest diversity of topography, the greatest isolation of ecological niches, and the most widely varying soil types (see Howard, 1973).

When the elevational and geographic ranges of the species of Jamaica, Cuba, and Hispaniola are studied (FIGURES 3–6; MAPS 1, 2; TABLES 4, 5), several interesting patterns emerge. Hispaniola, which has the highest mountains of the Greater Antilles, has well-developed zones of vegetation, especially in the Cordillera Central and the Massif de la Selle–Sierra de Baoruco (see Ciferri, 1936), and many of the taxa of *Lyonia* on this island are isolated by elevational barriers (FIGURES 5, 6). In the Cordillera Central the mountains are covered with a low-elevation *Pinus occidentalis* forest up to ca. 2000 meters, where there is a narrow zone of cloud forest. Above this zone there develops a unique high-elevation *P. occidentalis* forest with many shrubs and herbs that do not occur in the pine forests of the lower slopes.

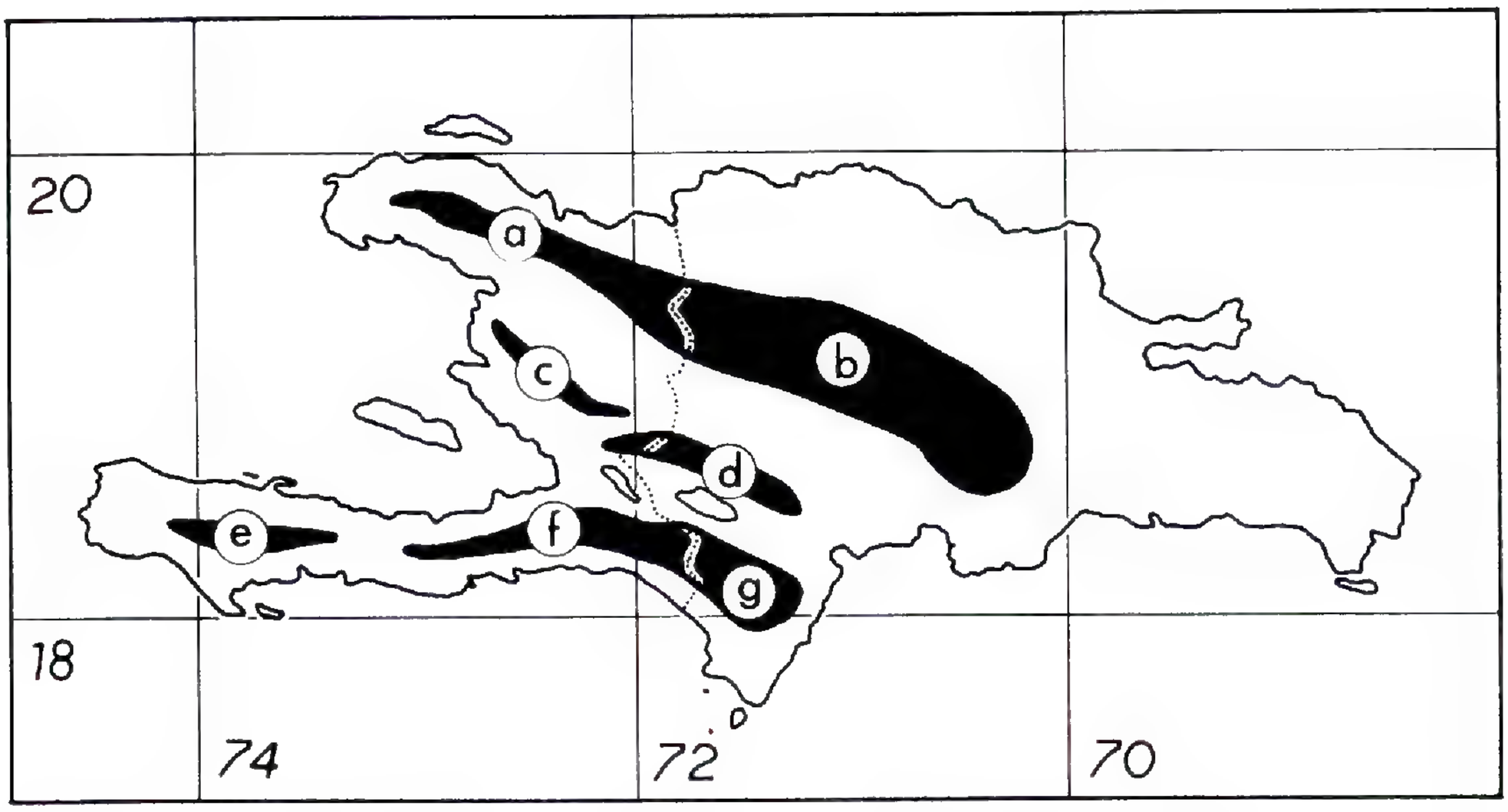
Lyonia has two major centers of endemism in Hispaniola: the Cordillera Central, where eight taxa are indigenous and five are endemic; and the Massif de la Selle–Sierra de Baoruco, with six taxa, three of which are endemic (MAP 2 and TABLE 4). These areas are also centers of diversity of other



MAP 1. Geographic areas of Cuba where *Lyonia* occurs (above, right): 1, Pinar del Río and Isla de Pinos; 2, Sierra de Trinidad and Sierra de Sancti Spiritus; 3, mountains of Oriente. Geographic areas of Oriente (below): a, Sierra de Nipe; b, Sierra de Mícara; c, Sierra de Cristal; d, Moa region; e, Sierra de Moa; f, Sierra de Toa; g, Sierra del Frijol; h, Baracoa region; i, Sierra Maestra; j, Gran Piedra.

genera (see Urban, 1923; Moscoso, 1943; Howard, 1973).

Many *Lyonia* species are isolated ecologically, with one taxon occurring at low elevations and a related one at higher altitudes. In the Cordillera Central this pattern is best illustrated by three pairs of species (see FIGURE 5): *Lyonia heptamera–L. buchii; L. tuerckheimii–L. rubiginosa* var. *costata;* and *L. urbaniana–L. tinensis.* The first-mentioned taxon of each of these three pairs characteristically occurs in the high-elevation pine forest, with the second in the isolated low-elevation pine forest. The altitudinal ranges of *L. heptamera* and *L. tuerckheimii* seem to overlap slightly with those of *L. buchii* and *L. rubiginosa* var. *costata,* respectively, since the high-elevation *Pinus occidentalis* forest begins at slightly different altitudes in various portions of the Cordillera Central due in part to edaphic factors and local wind currents. In the Massif de la Hotte, *L. rubiginosa* var. *costata* reaches elevations of ca. 2300 meters, but *L. tuerckheimii* does not occur; in the Cordillera Central, where both grow, *L. rubiginosa* reaches no higher than ca. 2100 meters. The elevational range of *L. rubiginosa* var. *costata* also appears to overlap that of *L. truncata,* a plant of dry, open pine forests, but actually these two related species do not occur together. In the Cordillera Central, *L. rubiginosa* extends only as low as ca. 1400 meters, while *L. truncata* var. *montecristina* grows as high as 1200 meters; in the Massif de la Selle, *L. rubiginosa* var. *costata* only extends as low as 1600 meters, and *L. truncata* var. *truncata* grows up to ca. 1600 meters (FIGURE 6)! *Lyonia rubiginosa* var. *costata* can be found as low as 1100 or 900 meters, but



MAP 2. Geographic areas where *Lyonia* occurs in Hispaniola: a, Massif du Nord; b, Cordillera Central; c, Massif des Cahos; d, Sierra de Neiba; e, Massif de la Hotte; f, Massif de la Selle; g, Sierra de Baoruco (including Monteada Nueva).

only in localities where *L. truncata* does not occur (i.e., Monteada Nueva or a few localities in the Massif du Nord). *Lyonia alpina,* probably related to *L. truncata* var. *truncata,* grows at much higher elevations in the Massif de la Selle than does the latter taxon. Other taxa of Hispaniola (e.g., *Lyonia truncata* var. *truncata–L. truncata* var. *montecristina; L. microcarpa–L. urbaniana*) are geographically isolated by their occurrence in mountain ranges that are separated by low areas of xerophytic vegetation in which *Lyonia* cannot grow. The former taxon of each pair occurs in the Massif de la Selle–Sierra de Baoruco, and the latter in the Cordillera Central. *Lyonia alainii* is also geographically isolated from the related *L. tuerckheimii* and *L. rubiginosa* var. *costata.*

The two Jamaican species, *Lyonia jamaicensis* and *L. octandra,* are also elevationally isolated, with *L. octandra* occurring in the elfin or cloud forests at the summits of the Blue Mountains and *L. jamaicensis* growing in the lower dry-slope forests (FIGURE 4).

In contrast to the taxa of Hispaniola and Jamaica, which have widely diverse elevational ranges, the taxa of Cuba (FIGURE 3), with a few exceptions, are rather uniform with respect to altitudinal distribution. Cuba is a large island with many semi-isolated mountain ranges (MAP 1), but these tend to be lower in elevation than those of Hispaniola.

In Cuba most of the taxa are limited to either Oriente or Pinar del Río, although one species (*Lyonia trinidadensis*) occurs in the mountains of Las Villas Province, near the center of the island. *Lyonia* is especially diverse in the mountains of Oriente, an area that is also the center of diversity for many other genera (see Seifriz, 1943; León, 1946; León & Alain, 1957; Alain, 1953, 1958; Howard, 1973). In Oriente, the Sierra de Cristal, Sierra

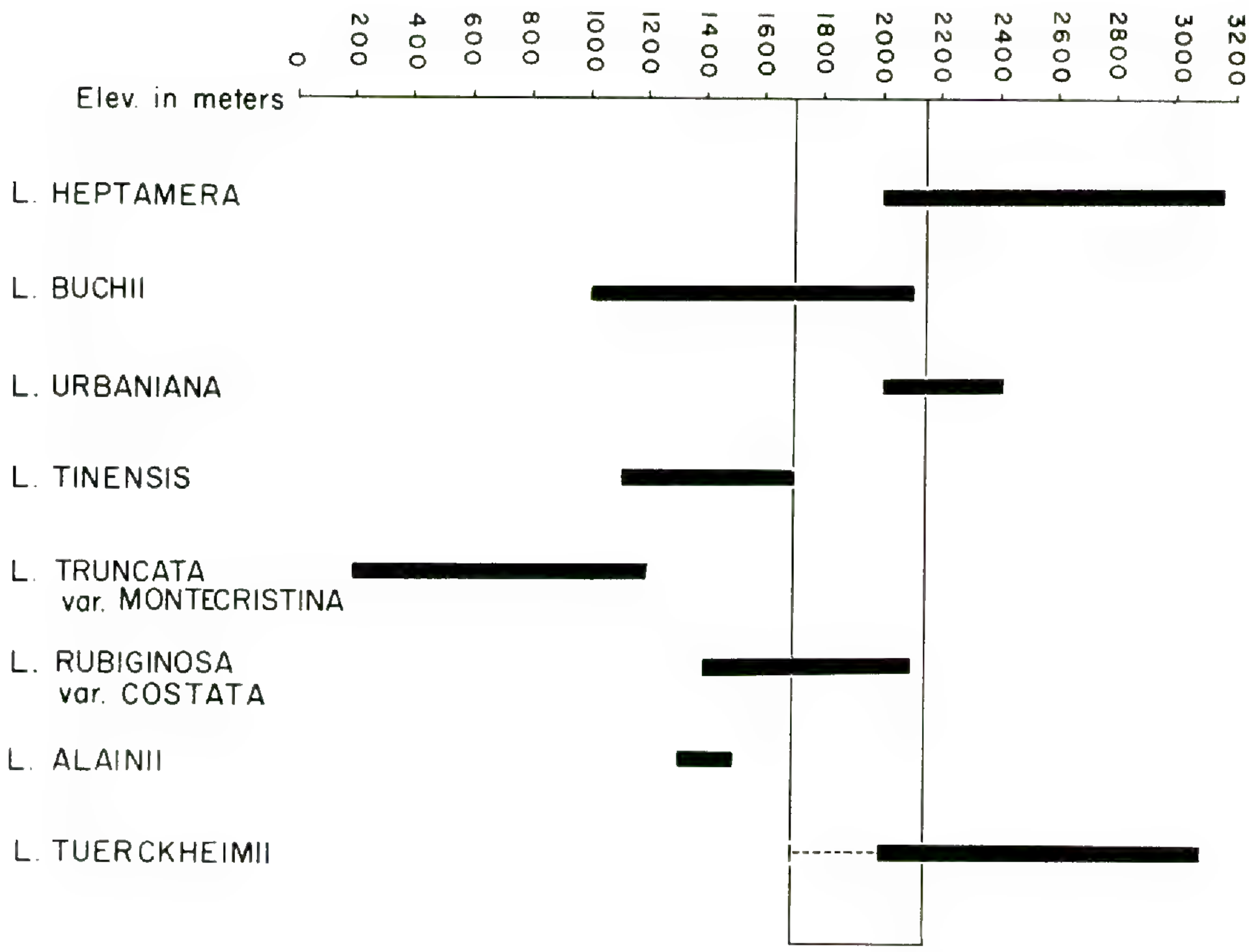


FIGURE 5. Altitudinal ranges of species and varieties of *Lyonia* occurring in Cordillera Central of Hispaniola. Vertical rectangle between ca. 1700 and 2150 m. indicates zone of cloud forests; forests dominated by *Pinus occidentalis* occur above and below this zone.

Maestra, Sierra de Nipe, Moa plateau, Sierra de Moa, Sierra de Toa, and Baracoa region show the greatest diversity in species of *Lyonia*, and most of these areas have at least one endemic taxon (MAP 1 and TABLE 5). This high degree of endemism in the various mountain ranges of Oriente was early noticed by E. L. Ekman, who collected extensively in Cuba and Hispaniola.

Because of the rather low elevation of many of these mountain ranges, there is less altitudinal variation and the species tend to be separated geographically. The geographically isolated areas of high endemism are often localities with unusual ecological conditions: for example, the *Pinus cubensis* forests and thickets on the red lateritic soils of such areas as Moa, Baracoa, and the Sierra de Nipe (overlying serpentine; see also Iturralde, 1976); the white-sand savannas of Pinar del Río; or the cloud forests, high-elevation thickets, or pine forests of the Sierra Maestra. Some geographically isolated Cuban taxa include *Lyonia nipensis* var. *nipensis*–var. *depressinerva; L. obtusa* var. *obtusa*–var. *longipes; L. latifolia* var. *latifolia*–var. *calycosa; L. elliptica–L. affinis; L. macrophylla–L. ekmanii; L. glandulosa* var. *glandulosa*–var. *revolutifolia* (both isolated from *L. toaënsis*). A few species, such as *L. affinis* and *L. latifolia* of the Sierra Maestra, may also be altitudinally isolated.

A few species of *Lyonia* (all of North America or eastern Asia) have very wide geographic and/or altitudinal ranges and are adapted to a wide range of ecological conditions. These species include *L. mariana, L. lucida, L. ligustrina, L. villosa,* and *L. ovalifolia* (FIGURE 7). It is interesting that in sect. LYONIA there has been extensive speciation within the topographically and ecologically diverse West Indian islands, while in sect. PIERIDOPSIS there has not been similar speciation in the equally or even more diverse mountains of eastern Asia. The magnitude of morphological variation within the two groups is roughly similar, but in sect. LYONIA the variation is discontinuous, thus allowing the recognition of many species, while in sect. PIERIDOPSIS it tends to be continuous, allowing—at most—the recognition of intergrading geographic varieties. This difference in pattern of variation is possibly the result of genetic or historico-climatic differences between these two groups.

Within eastern Asia, the greatest diversity is reached in Yunnan Province, China, and adjacent regions (MAP 3), where the most primitive species (*Lyonia compta* and *L. chapaënsis*) also occur. The distribution of *Lyonia* sect. PIERIDOPSIS illustrates the classic Sino-Japanese distribution pattern shown by many mesophytic temperate genera. Hara (1966) has listed 128 examples of taxa showing this pattern, including the ericaceous genera *Monotropa* L., *Monotropastrum* H. Andres, *Enkianthus* Lour., *Lyonia,* and *Pieris.* Some species occurring throughout the full range from Japan to the Himalayas show little variation, but most either vary infraspecifically over that area (e.g., *L. ovalifolia*) or have closely related species in Japan and the Himalayas.

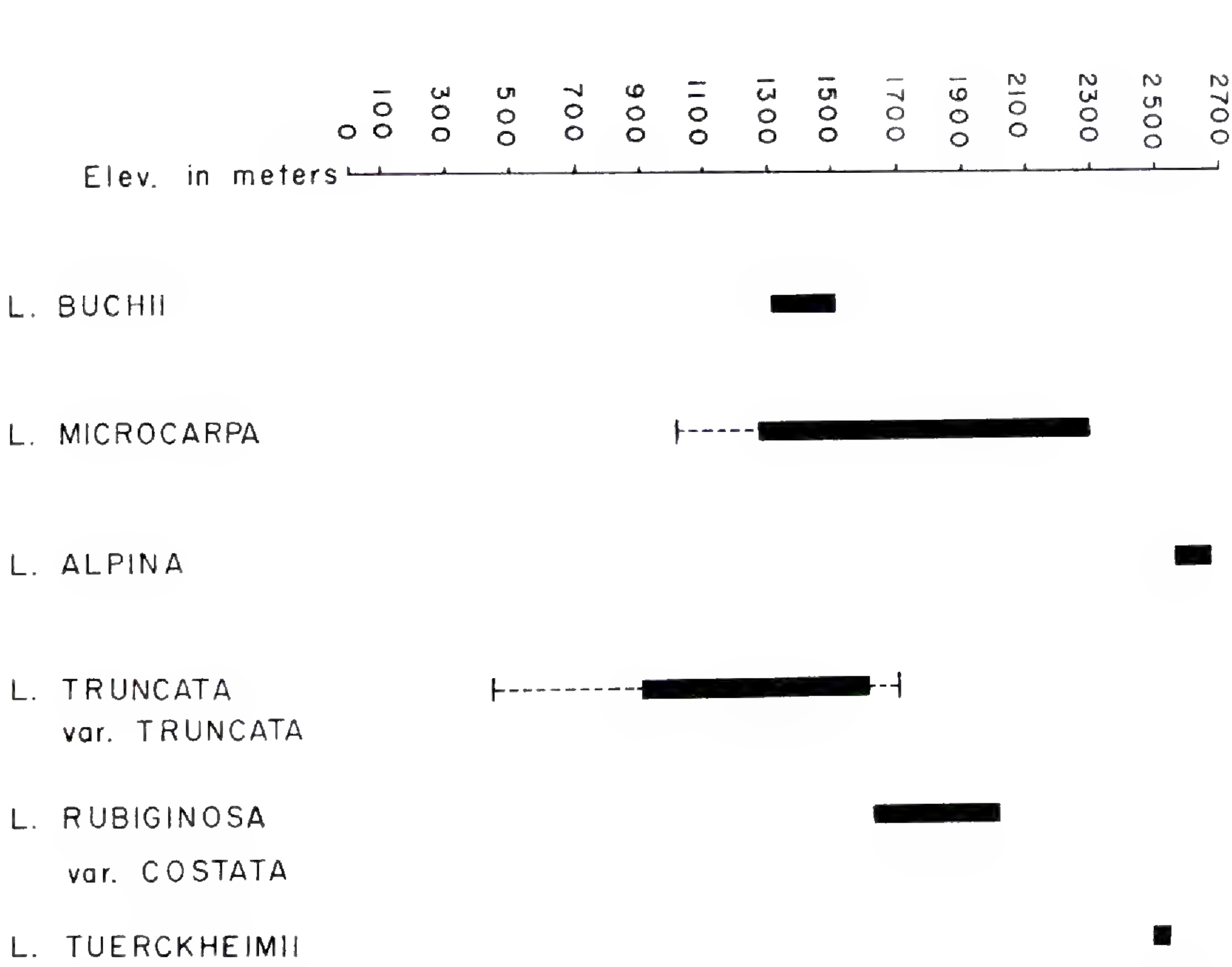


FIGURE 6. Altitudinal ranges of species and varieties of *Lyonia* occurring in Massif de la Selle–Sierra de Baoruco, Hispaniola.

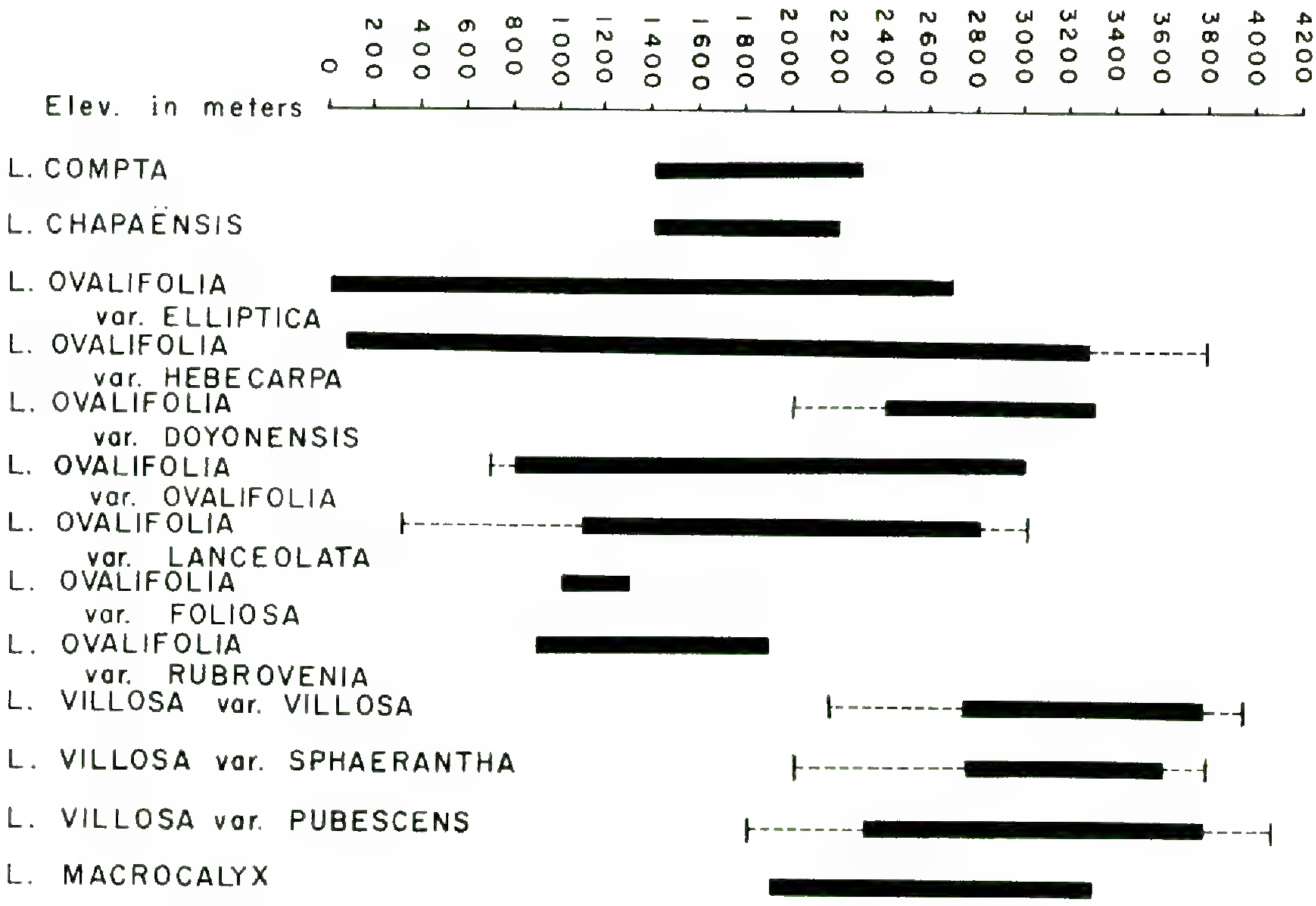
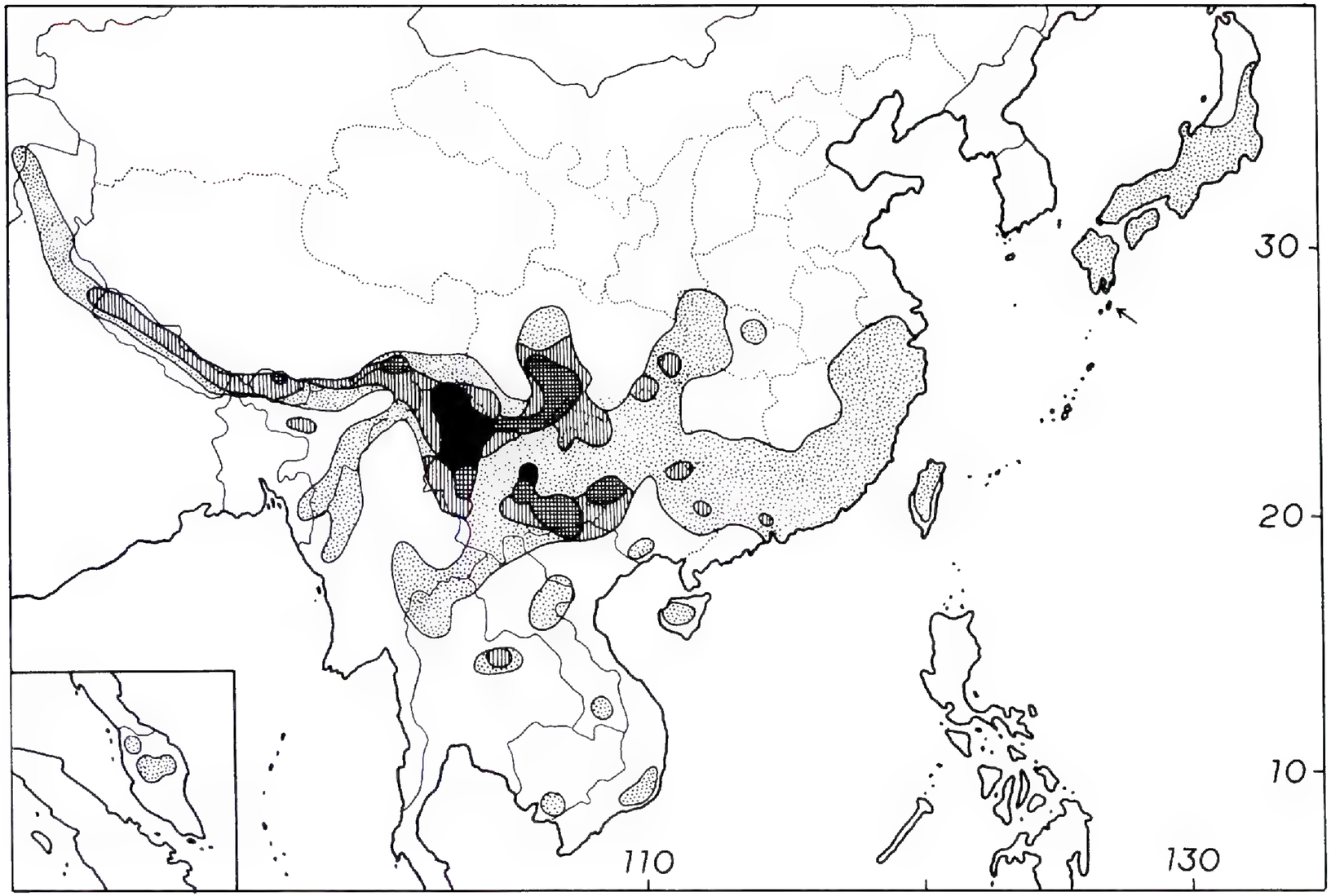


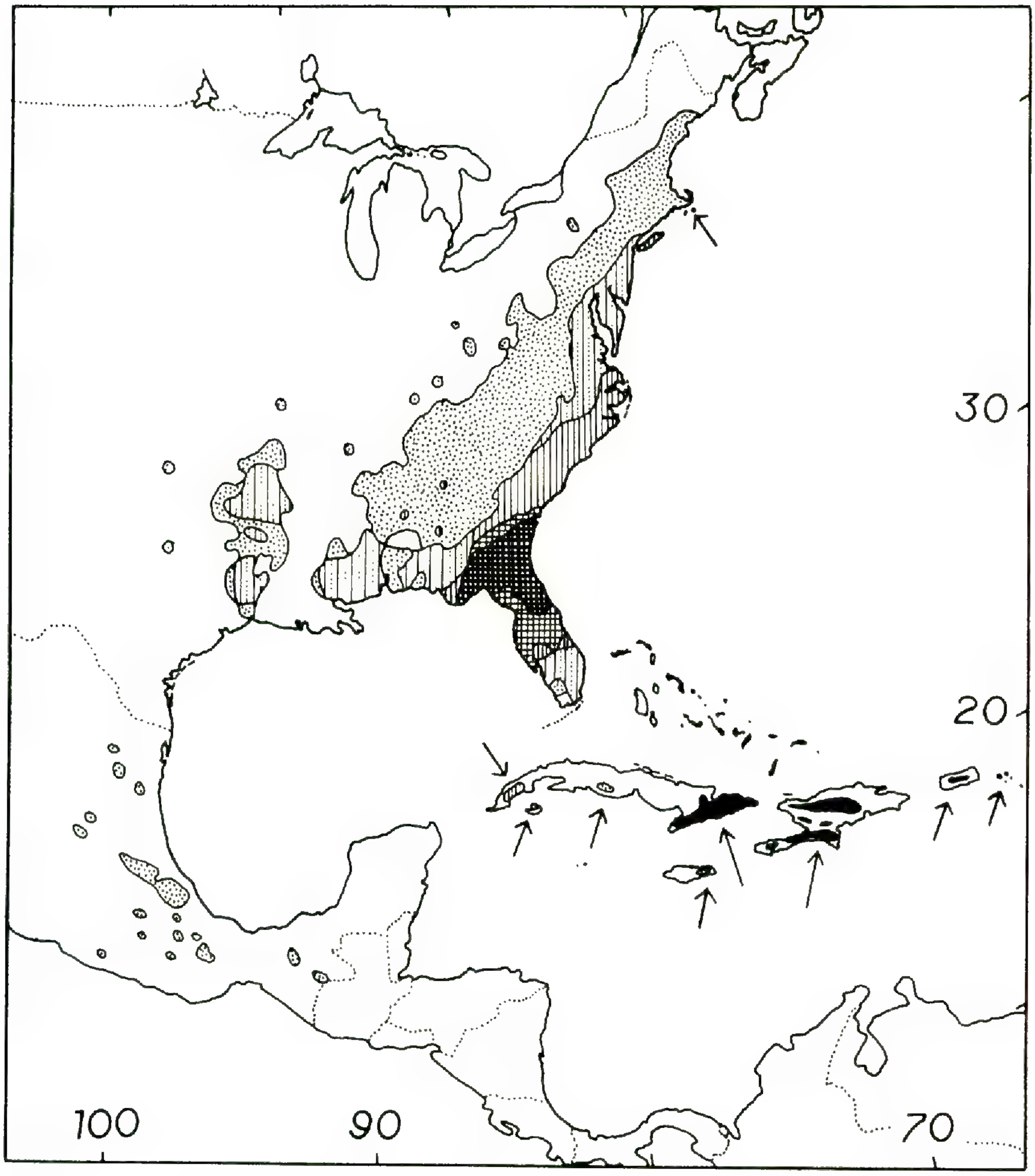
FIGURE 7. Altitudinal ranges of taxa of *Lyonia* sect. PIERIDOPSIS.

The center of diversity of many of these genera is found in Yunnan, and many also occur in North America. The morphological variation within *L. ovalifolia* is greatest in Yunnan, where four varieties are found; the varieties tend to be altitudinally and/or ecologically isolated. *Lyonia villosa,* a species closely related to *L. ovalifolia,* occurs only from the western Himalayas to Szechwan and Yunnan and usually grows at higher elevations than does *L. ovalifolia* (FIGURE 7).

In continental North America, the greatest number of *Lyonia* species is found in northern Florida, southeastern Georgia, and southern South Carolina, where *L. mariana, L. lucida, L. ligustrina, L. ferruginea,* and *L. fruticosa* all occur (MAP 4). These species are all clearly demarked and can often be found growing nearly side by side, although *L. lucida* is usually in wetter sites than *L. mariana,* and *L. ferruginea* tends to grow in more shaded and/or well-drained areas than *L. fruticosa.* It is probable that the geographic range of *Lyonia* in continental North America has not always been as it is today. There is now considerable evidence that significant vegetational displacement took place during times of glacial advance (Frey, 1953; Whitehead & Barghoorn, 1962; Watts, 1970; Whitehead, 1972; Davis, 1976). The full glacial pollen assemblages in these studies conducted in the southern United States are often quite different from modern pollen assemblages of the same region. Whitehead (1972), in his study of the environmental history of the Dismal Swamp, states that *Taxodium-Nyssa* forests have only characterized the swamp for the past 3500 years; before that time, the region was occupied by more northern forest types. *Lyonia lucida* and *L. ligustrina* var. *foliosiflora,* which



MAP 3. Generalized distribution of *Lyonia* sect. PIERIDOPSIS, showing center of diversity in Yunnan, China. Pattern indicates number of taxa present: stipples, 1; vertical lines, 2; cross hatching, 3; solid black, 4 to 7.



MAP 4. Generalized distribution of *Lyonia* sects. LYONIA, MARIA, and ARSENOCOCCUS, showing centers of diversity in Greater Antilles and southeastern United States. Pattern indicates number of taxa present: stipples, 1; vertical dotted and solid lines, 2; vertical solid lines, 3; light cross hatching, 4; heavy cross hatching, 5; solid black, 6 to 10.

today reach their northernmost point in the Dismal Swamp, have likely rather recently migrated into this region from the south. Disjunct populations of *L. lucida* are found around several ponds in Bartow Co., Georgia, northwest of Atlanta. Watts (1970) found that familiar southern tree genera such as *Liquidambar* and *Nyssa,* and Coastal Plain species such as *Itea virginica* and *Psilocarya nitens,* migrated into the vicinity of these ponds in postglacial times. It is likely that *L. lucida, L. mariana,* and *L. ligustrina* have all moved northward following the Wisconsin Ice recession. *Lyonia ligustrina*

var. *ligustrina* is most diverse in the southern Appalachians but extends northward to southern Maine; *L. mariana* seems to have followed the Coastal Plain northward as far as southeastern Connecticut and Long Island, New York. Braun (1947), however, felt that major changes of vegetation were limited to the Coastal Plain, with the floral composition of the Appalachian highlands having been only slightly affected, and Graham (1973, p. 304) states that "a conservative view of vegetational history in the southeast would be a community definitely influenced by fluctuating Pleistocene environments . . . but . . . still retaining the general aspect and composition of the deciduous forest in a regional sense." It is likely that there was some mixing of northern and southern taxa during the Pleistocene.

No species of *Lyonia* occurs in the Mississippi embayment region, and *L. mariana* occurs disjunctly in the Atlantic Coastal Plain and in eastern Texas, Arkansas, and several neighboring states. There are a number of plants that show similar dichotomous distributions; some are listed by Duke (1961) and by Gillis (1971).

ECOLOGY

The genus occurs in a wide variety of habitats, but characteristically prefers acid soils (pH sometimes as low as 2.8, as in *Lyonia octandra;* Tanner, 1977). Only rarely do species occur over limestone, but *L. truncata* and *L. microcarpa* have been seen growing in the lateritic soil filling the cracks of eroded limestone rocks, and *L. rubiginosa* var. *costata* growing on organic soil developed over a limestone bedrock (pers. obs.). Many Cuban species (e.g., *L. nipensis, L. obtusa, L. glandulosa, L. macrophylla*) occur on red lateritic soils developed by the weathering of underlying serpentine rocks. Other species, such as *L. heptamera, L. urbaniana, L. tinensis, L. tuerckheimii,* and *L. rubiginosa,* of the Cordillera Central (Hispaniola), grow on soils derived from igneous rocks. Most of the species of the southeastern United States and of western Cuba occur on siliceous soils. Species such as *L. mariana, L. ligustrina,* and *L. lucida* also grow in highly organic soils such as those of bogs and swamps. Several Caribbean taxa (especially those of cloud forests, such as *L. octandra* and *L. rubiginosa*) can also be found in organic soils.

The Caribbean species occur in moist montane or cloud forests, high- or low-elevation pine forests, savannas, or thickets. They range in altitude from nearly sea level to 3175 meters. Thus, *Lyonia heptamera* can be found at the top of the highest peak of Hispaniola (Pico Duarte, 3175 meters), while *L. myrtilloides* and *L. lucida* grow near sea level in Pinar del Río, Cuba, and *L. macrophylla* occurs just above sea level near Moa, Cuba. The region around Moa, because of its lateritic soil, has many normally montane species growing just above sea level. In Hispaniola *L. truncata* var. *montecristina* has been collected from elevations as low as 100 meters (FIGURE 4).

The continental North American and eastern Asian species of *Lyonia* are often found in a wide range of habitats. *Lyonia ovalifolia,* for example, occurs in subtropical *Castanopsis* forests; warm-temperate forests of *Pinus*

and/or *Quercus;* cold-temperate forests of *Tsuga, Abies,* or *Picea;* dry *Rhododendron* thickets; mixed deciduous forests; or dwarf cloud forests. *Lyonia ligustrina* also occurs in diverse ecological situations, such as moist *Taxodium* swamps, shrub bogs, *Pinus* and/or *Quercus* woods, grassy balds, thickets, and acid bogs and swamps. Both species can be found in dry, rocky situations or just above the standing water of bogs or swamps, and both often occur in ecotones such as the edge of a forest, or the margin of a pond or a swamp.

Species of *Lyonia* sprout readily after cutting or fire since they are very tolerant of disturbance. Several species (e.g., *L. fruticosa, L. mariana,* and *L. ovalifolia*) often seem to respond favorably to fires, and most taxa react positively to at least slight disturbance because they are light-loving plants and become more abundant when the overstory trees are cut. In addition, the taxa, except for those of the Greater Antilles, have the ability to spread vegetatively by underground rhizomes. Undisturbed habitats within the Caribbean and in Mexico are fast disappearing, and it is thus fortunate that most species of *Lyonia* are only little harmed by slight human disturbance. Shrubs of *L. buchii, L. rubiginosa,* and *L. truncata* grow in the Dominican Republic along roadsides where the surrounding vegetation is cut and heavily grazed, and *L. truncata* also occurs on reclaimed aluminum mine areas near Aceitillar (pers. obs.); if the disturbance is strong enough, however, even *Lyonia* will be eliminated.

As the human population of these areas increases, one has to go higher and higher into the mountains to reach undisturbed and floristically diverse habitats, and the danger of extinction, especially for narrowly endemic or uncommon taxa, is increasing dramatically. *Lyonia rubiginosa* var. *rubiginosa,* which is endemic to the island of St. Thomas, may already be extinct, since it was last collected in 1887; attempts to relocate it in 1975 were unsuccessful. Other rare or endangered taxa are *L. rubiginosa* var. *stahlii* (Puerto Rico), *L. alpina* (Haiti), *L. alainii* (Dominican Republic), *L. toaënsis* (Cuba), *L. maestrensis* (Cuba), *L. elliptica* (Cuba), and *L. ekmanii* (Cuba).

TAXONOMIC CRITERIA

Systematic relationships within the Andromedeae have often been obscured by the inconsistent use of characters, the emphasis on certain "key" characters, the use of characters that are so variable that only little taxonomic value can be assigned to them, and the neglect of many useful morphological and anatomical features. In this study, as many characters as possible from all parts of the plant have been employed, and inter- and intraspecific variation have been carefully determined.

Usually no single character can be employed throughout the genus, so different species are separated by different sets of characters. Morphological entities that show a consistent complex of character states (i.e., have no major internal discontinuities) and that are separated from other similar entities by a consistent morphological gap are considered to be species. They have definite geographic distributions and ecological preferences and are often

rather uniform in flower and/or fruit morphology. Species are isolated by differences in their ecological and/or altitudinal characteristics, geographic distribution, flowering time, and floral morphology and/or genetic composition. The term "variety" has been used for the morphologically distinctive subunits comprising widespread and often ecologically variable species (see Fernald, 1940; Fosberg, 1942; Weatherby, 1942; but also Clausen, 1941). These varieties are more or less geographically and/or ecologically isolated but intergrade where they come into contact and are probably completely interfertile. Varieties have slight morphological gaps between them, tending to differ in habit, leaf morphology, indumentum, or slight anatomical peculiarities. Any two varieties of a species are usually more similar in absolute number of characters than any two species within that section. The varieties of a few Caribbean species do not naturally come into geographic contact, and thus the taxonomic rank of these entities is somewhat arbitrary. If, however, two allopatric Caribbean taxa differ from each other in only a few vegetative characters, with only a very slight morphological gap between them, they have here been treated as varieties of a single, more variable species.

The taxonomic usefulness of (and the variation within) the various characters used in this monograph are discussed below.

Habit

The species of *Lyonia* vary from small, prostrate to erect shrubs to moderate-sized trees up to 18 meters tall. *Lyonia mariana* is distinctive in that it is a very small, erect shrub that never exceeds 1.5 meters in height. Taxa growing at high altitudes are often dwarfed (e.g., *L. villosa* often forms low (0.5–1.5 meters) thickets at high elevations in the Himalayas, and *L. alpina* only reaches ca. 0.5 meters on the highest peaks of the Massif de la Selle in Haiti). The genus is almost exclusively terrestrial, but occasional individuals of *L. octandra* have been seen growing as epiphytes on trees in moist montane forests (pers. obs.). Although the habit of many species is extremely variable, it may be consistent; thus, for example, *L. buchii* can be distinguished from *L. heptamera*, *L. ferruginea* from *L. fruticosa*, and *L. rubiginosa* from *L. tuerckheimii*, because the first of each of these pairs is characteristically arborescent and the second a low to erect shrub. The branching pattern (including internode length, density of branching, and orientation of branchlets), although variable, is also useful and helps in distinguishing the varieties of *L. truncata* from each other, *L. ferruginea* from *L. fruticosa*, and *L. urbaniana* from *L. microcarpa*.

The twigs vary from slender to very stout, from round to strongly angled, and from nearly glabrous to densely pubescent. Most species of sect. Lyonia have at least moderately ridged twigs, but *Lyonia mariana*, *L. ligustrina*, and the Asian species often have round or only very slightly angled branches, and *L. lucida* is unusual in having strongly 3-angled stems. The stoutness of the twigs is a useful character in separating *L. tuerckheimii* and *L. rubiginosa* var. *costata* but varies infraspecifically in some species, such as *L. heptamera* and *L. buchii*.

The bark is always longitudinally furrowed and is sometimes shredded; it varies in color from gray to reddish brown. It is occasionally taxonomically useful, as in distinguishing *Lyonia jamaicensis* from *L. octandra*, and *L. heptamera* from older individuals of *L. buchii*. There is much variation in the density and prominence of the vertical furrows.

Species such as *Lyonia heptamera, L. tuerckheimii, L. truncata*, and possibly

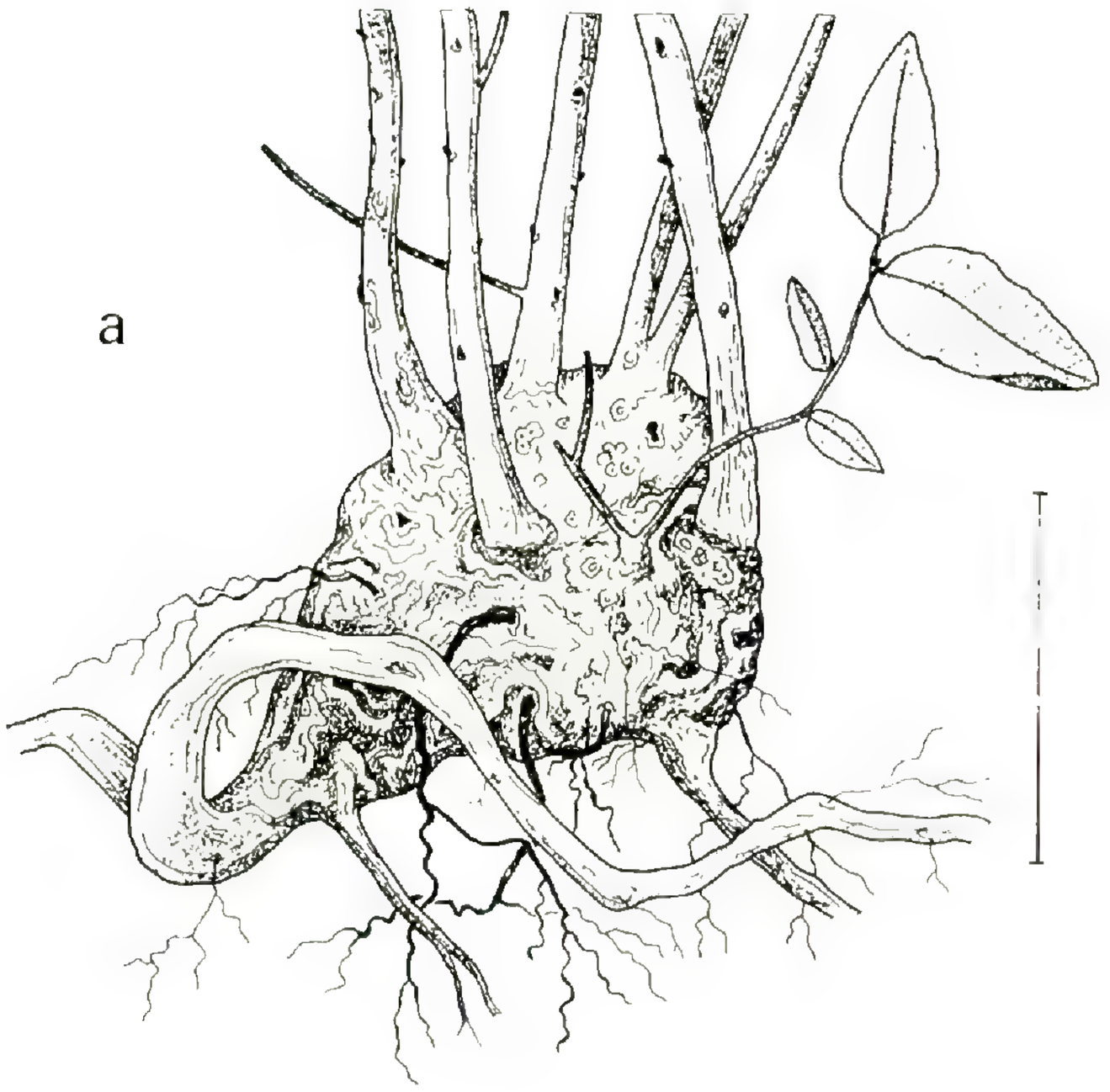


FIGURE 8. Roots and burls: a, *Lyonia heptamera*, woody underground burl (scale = 4 cm.); b, *L. ferruginea*, elongated woody burl producing underground rhizomes (scale = 10 cm.).

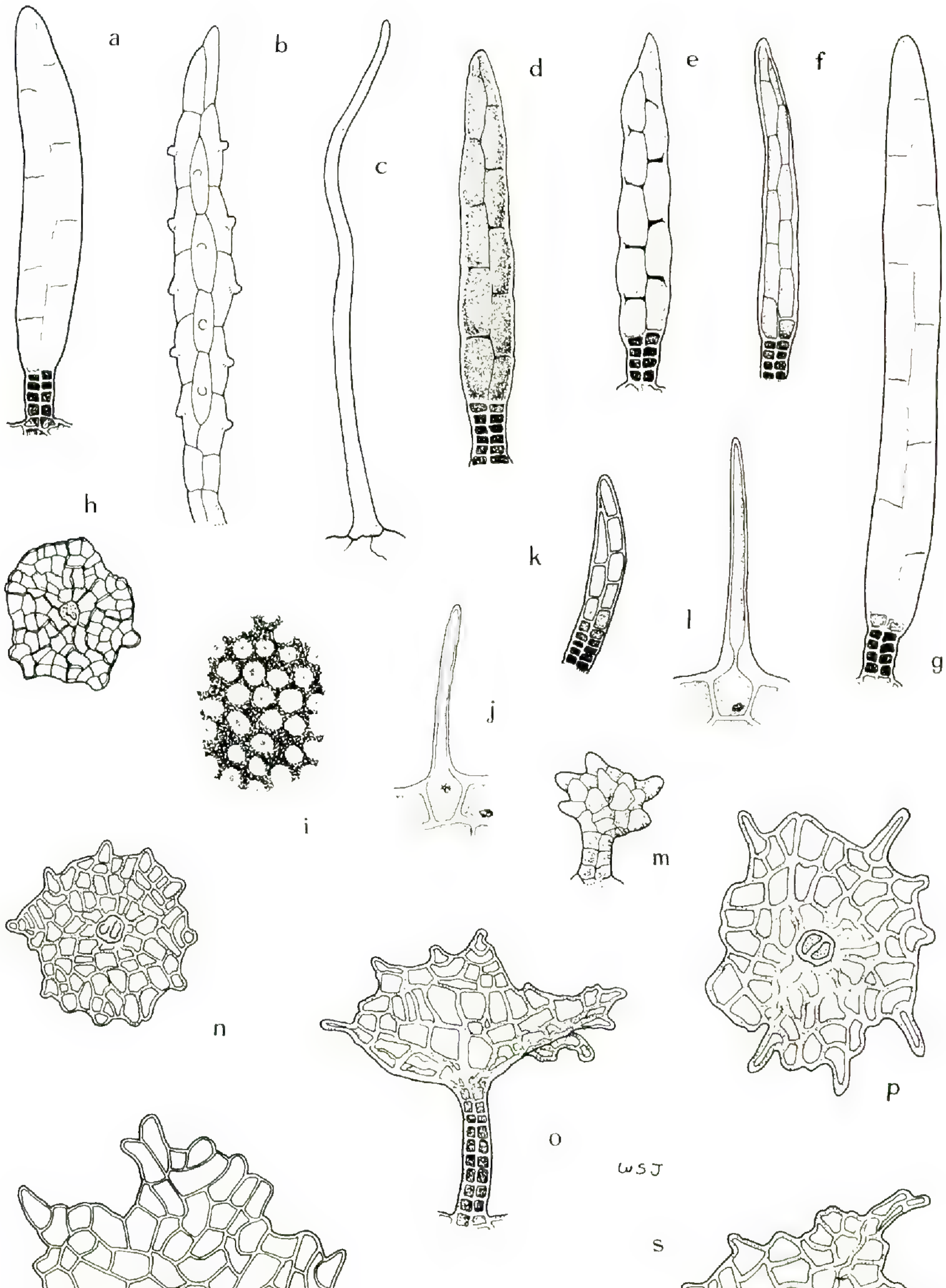
L. urbaniana frequently produce rounded, woody burls just below the soil surface (FIGURE 8). These burls are often the source of young shoots, especially when the plant is cut or is damaged by fire, and are commonly developed even in very young plants. *Lyonia ferruginea, L. fruticosa,* and *L. squamulosa* produce large, elongated burls (to ca. 10 dm.), which form both erect shoots and horizontal underground rhizomes (FIGURE 8). This rhizome network is often especially extensive in *L. fruticosa* and *L. squamulosa,* which can form large clones. In contrast, the rhizomes of *L. ferruginea* are usually few and fairly short. These three species are the only taxa of sect. LYONIA that are known to produce rhizomes. *Lyonia ligustrina, L. lucida, L. mariana,* and probably all the Asian species also spread vegetatively by rhizomes. These rhizomes have small, scalelike leaves with small axillary buds and initially develop adventitious roots only immediately above the buds (FIGURE 11). The rhizomes can continue growth underground or can turn upward and form vertical shoots with normal photosynthetic leaves. Several species form extensive colonies by means of this vegetative reproduction.

Care must be taken when dealing with habit characters because they are often strongly influenced by environmental conditions. The potential to produce rhizomes may not be realized in all situations, and shoot orientation often varies with habitat. For example, in moist, shaded conditions *Lyonia lucida* has beautifully arching branches; in sunny, seasonally dry environments it develops rigidly ascending branches similar to those of *L. fruticosa,* which also occurs in such habitats. However, the difference between *L. fruticosa* and *L. ferruginea* (rigidly ascending vs. lax branchlets) is maintained even under uniform greenhouse conditions.

INDUMENTUM

The indumentum of *Lyonia* is of three distinct types (FIGURES 9, 10): unicellular hairs; multicellular, biseriate-stalked, swollen-headed glandular hairs or peltate scales; and papillae. Many ericaceous genera have multicellular, glandular-headed hairs, and nearly all have unicellular hairs.

The peltate scales of *Lyonia* sect. LYONIA at first glance appear to be very different from the swollen-headed hairs of sects. PIERIDOPSIS, ARSENOCOCCUS, and MARIA, but both have biseriate stalks, occur in similar positions on the plant, and have similar developmental patterns (FIGURE 9); they are probably derived from a common hair type. These two types of multicellular hairs occur essentially all over the plant—on the twigs, buds, leaves, pedicels, calyx lobes, corolla (outer surface), and ovary. The density, color, persistence, and structure of the peltate scales are often very useful taxonomic characters and help to distinguish between various West Indian species. Unfortunately, the comparable characteristics of the swollen-headed hairs are either too variable or too uniform to be useful in distinguishing taxa among the Asian and North American species. An important exception is that the multicellular swollen head of these hairs is elongate in sects. PIERIDOPSIS and ARSENOCOCCUS but short in sect. MARIA. In addition, the ovary in sect. ARSENOCOCCUS is often moderately covered with swollen-headed hairs, while the ovaries in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sect. PIERIDOPSIS usually lack such hairs. The swollen head of these multicellular hairs is often reddish in sect. MARIA but varies from greenish or clear to reddish in sects. ARSENOCOCCUS and PIERIDOPSIS.

The margin of the peltate head of the scales of sect. LYONIA varies from entire to irregular or fimbriate. The scales range in color from golden to rusty (usual condition), tan, or dark brown; in many taxa they become whitish as the leaves age. Their stalks can be elongated or rather short and can be impressed into the abaxial leaf epidermis or not. The scales on a single plant may be of one morphological type or may be dimorphic in size, persistence, or structure. On the abaxial leaf surface they vary from persistent to deciduous, but they are almost always deciduous on the adaxial surface. Scales may be absent from a given plant part (e.g., the adaxial surface of the calyx lobes) in some taxa and present on the same part in others. Finally, the density of scales on leaves, corolla, calyx lobes, and other plant parts is often taxonomically useful. When taxa are compared, it is important to look at fully developed leaves, since the young shoots are always more densely lepidote than the mature ones of the same plant. A few taxa in which the above-mentioned variations are important are discussed here; others are evident in the keys. The related species *Lyonia macrophylla* and *L. obtusa* are easily distinguished by the density of ferrugineous scales on the abaxial surface of their leaves. Although most species have only sparsely lepidote corollas and lack scales on the adaxial surface of the calyx lobes, *L. nipensis* and *L. latifolia* are distinctive in having densely lepidote corollas, and the latter is unusual in that its calyx lobes are densely lepidote on both surfaces. Some species can be easily distinguished by the color of their scales: brownish in *L. urbaniana* and *L. tinensis,* more or less orange in *L. microcarpa,* and golden in *L. latifolia.* The scales of *Lyonia nipensis* var. *depressinerva* and *L. ferruginea* are characteristically of two distinct sizes; those of their relatives (*L. nipensis* var. *nipensis* and *L. fruticosa,* respectively) are usually all large. *Lyonia obtusa* and *L. alainii* have nearly entire-margined scales, while their relatives have scales that are usually irregular- or fimbriate-margined.

The distribution of unicellular hairs is of taxonomic interest, although their morphology is usually rather invariable. These hairs, which are composed of a single, elongated cell (FIGURE 9), almost always occur singly; however,

FIGURE 9. Unicellular and multicellular hairs and peltate scales, × 150 (all except b, f, k, and m from abaxial leaf surface): a, *Lyonia ligustrina* var. *ligustrina,* multicellular hair; b, *L. villosa* var. *pubescens,* multicellular hair from filament of *Forrest 28708* (E); c, *L. ovalifolia* var. *hebecarpa,* unicellular hair; d, *L. compta,* multicellular hair; e, *L. ovalifolia* var. *rubrovenia,* multicellular hair; f, k, *L. ligustrina* var. *ligustrina,* developing multicellular hairs; g, *L. ovalifolia* var. *hebecarpa,* multicellular hair; h, p, *L. ferruginea,* peltate scales; i, *L. macrocalyx,* papillae; j, *L. ligustrina* var. *ligustrina,* unicellular hair; l, *L. mariana,* unicellular hair; m, *L. ferruginea,* developing peltate scale; n, *L. truncata,* peltate scale; o, s, *L. heptamera,* peltate scale; q, *L. latifolia,* peltate scale; r, *L. alainii,* peltate scale.

occasional paired hairs have been seen. The presence of a dense layer of unicellular hairs on the abaxial leaf surface is characteristic of many species of sect. LYONIA, but these hairs are lacking in other species (see TABLES 7, 8). Although *Lyonia mariana, L. ligustrina,* and several Asian species have similar unicellular hairs along the veins of their lower leaf surfaces, none has this characteristic dense layer. The presence of this dense pubescence is not affected by environmental conditions, but it is slightly influenced by the age of the plant, in that seedlings and juvenile shoots tend to lack these hairs or to have only a sparse covering of them. Nearly all species of *Lyonia* have unicellular hairs on the midvein of the adaxial leaf surface; within sect. LYONIA, the Cuban species (and *L. tuerckheimii*) often have unicellular hairs on the midvein of the abaxial surface as well. Similar hairs often occur on the veins of both leaf surfaces in *L. villosa, L. ovalifolia, L. ligustrina,* and *L. mariana*. The density of unicellular hairs on the twigs is variable in most species, but in certain cases it helps to distinguish between closely related species such as *L. tuerckheimii* and *L. rubiginosa,* or *L. jamaicensis* and *L. octandra*. The density of such hairs on the bracts, bracteoles, pedicels, calyx lobes, and capsules is usually not of taxonomic importance.

The leaves of a few Asian taxa (*Lyonia macrocalyx, L. villosa,* and *L. ovalifolia* vars. *doyonensis* and *ovalifolia*) are either occasionally or always papillose. The papillae are projections of the cells of the lower leaf epidermis and sometimes also of the epidermal cells of the calyx lobes (FIGURE 9). Sometimes visible only under the high-power dissecting microscope, they are often more obvious in taxa with glaucous abaxial leaf surfaces.

BUDS

The buds of *Lyonia* are ovoid and range in length from only 1–2 mm. (in most of the Caribbean species) to ca. 12 mm. (in many Asian taxa). The buds of nearly all species have two small to large imbricate scales (which are modified leaves; FIGURE 10). In *L. mariana* and occasionally in *L. lucida,* the buds have only two visible scales when very young but soon expand to reveal additional scales; the buds are glabrous or almost so. The buds of sect. LYONIA are usually densely lepidote; those of sects. PIERIDOPSIS and ARSENOCOCCUS are glabrous to moderately covered with unicellular hairs and often have a few multicellular ones. The buds of species in the last two sections often become reddish in autumn.

LEAVES

In all species of *Lyonia,* the leaves are alternate, and the lowermost ones of the shoots are typically small and scalelike. Species such as *L. mariana, L. ligustrina, L. ovalifolia,* and *L. villosa* are deciduous, with chartaceous to coriaceous leaves that often turn reddish in autumn. The leaves of *L. compta, L. lucida,* and all species of *Lyonia* sect. LYONIA are evergreen, persisting for as long as three years, and are frequently extremely coriaceous. Petiole length, although often rather variable, is sometimes taxonomically useful. Lamina size varies dramatically within many taxa, and this variability has led to the description of many species that cannot be maintained when

the total range of variation is considered. Variation is especially great in the Asian and North American species of the genus. For example, the mature leaves of *L. ovalifolia* vary from ca. 21 cm. long and 12 cm. wide to only 2.5 cm. long and 1 cm. wide. However, several taxa in sect. LYONIA (e.g., *L. urbaniana, L. microcarpa*) consistently have leaves only up to 3 or 4 cm. long.

The shape of the leaf, especially of the apex, also varies greatly, sometimes within single populations or even on an individual plant. Many Caribbean

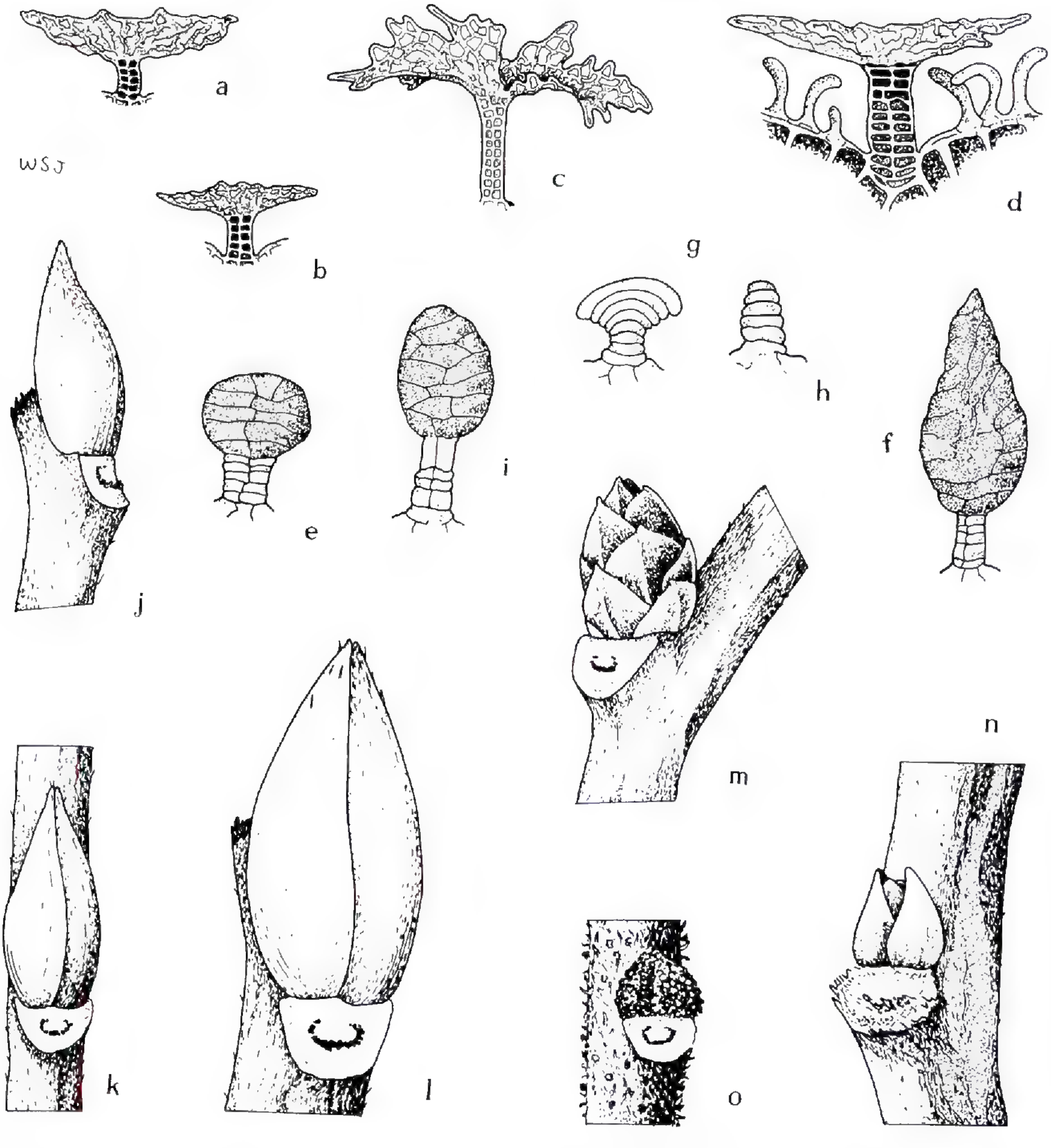


FIGURE 10. Hairs and buds. a–i, hairs, from abaxial leaf surface, × 150: a, *Lyonia truncata,* peltate scale; b, *L. alainii,* peltate scale; c, *L. latifolia,* peltate scale; d, *L. ferruginea,* peltate scale and adjacent unicellular hairs; e, f, *L. lucida,* multicellular hairs; g, h, *L. lucida,* developing multicellular hairs; i, *L. mariana,* multicellular hair. j–o, buds, × 5: j, k, *L. ligustrina* var. *ligustrina;* l, *L. ovalifolia* var. *ovalifolia;* m, *L. mariana;* n, *L. lucida;* o, *L. fruticosa.*

species (e.g., *L. truncata, L. rubiginosa, L. latifolia, L. nipensis*) have leaves that vary from rounded to truncate, obtuse, or acute (and in some, even acuminate) at the apex. In populations of *L. ferruginea* and *L. fruticosa* on the Coastal Plain in Georgia and Florida, plants with rounded leaves and plants with acute leaves have been seen growing side by side (pers. obs.). The variation in leaf apex is slightly less in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS, but even in these groups it is often considerable. *Lyonia ovalifolia, L. villosa,* and *L. ligustrina* are particularly variable (FIGURES 21–28). Narrowly to widely obovate, ovate, or elliptic leaves are commonly found in the same species. However, a few taxa have unusually shaped leaves. The lamina of *L. heptamera* is cordate at the base, while that of *L. buchii* is cuneate—a difference that helps in distinguishing the two species. Similarly, the narrowly elliptic lamina of *L. glandulosa* var. *revolutifolia* can be distinguished from that of var. *glandulosa,* which is narrowly to widely obovate. In spite of the wide range of variation in leaf size and shape or in apex type that is found in many taxa, these characters employed with caution are often useful in differentiating the varieties of several Eastern Asian and West Indian species; they also help to separate some species (e.g., *L. microcarpa* from *L. urbaniana,* and *L. compta* or *L. chapaënsis* from the remaining Asian species). The leaf blade is more or less flat in most species, but it may be strongly recurved as in *L. nipensis* var. *depressinerva, L. glandulosa,* and *L. ferruginea.* The margin is at least occasionally slightly revolute in most species, but in a few it is strongly so. It is entire in all taxa of sects. MARIA and PIERIDOPSIS, although slightly undulate in *L. chapaënsis.* The leaves of *L. ligustrina* are minutely serrulate, and those of species of sect. LYONIA vary from entire, to obscurely toothed, to irregularly and clearly toothed or notched. The teeth are usually more prominent toward the distal end of the blade, and each tooth has a multicellular, swollen-headed hair (or, in sect. LYONIA, a peltate scale) on its distal side. The leaves of Cuban and Jamaican species tend to be entire margined, while those of Hispaniolan and Puerto Rican species are often distinctly toothed. The number of teeth is helpful in differentiating *L. rubiginosa* var. *costata* from var. *stahlii,* and *L. maestrensis* from several other Cuban species.

The veins of the leaves of most species are either only very slightly raised above the surface or slightly depressed. However, in some species (*Lyonia nipensis* var. *depressinerva, L. ferruginea, L. glandulosa, L. rubiginosa* var. *costata, L. latifolia* var. *latifolia, L. buchii,* and *L. heptamera*) the first-, second-, and sometimes even third- or higher-order veins are often prominently impressed into the adaxial leaf surface (see FIGURES 35, 44, and 50). *Lyonia heptamera, L. buchii, L. urbaniana, L. tinensis,* and *L. microcarpa* are unusual in that the veins on the abaxial leaf surface form a raised network, thus forming small pockets in the surface of the leaf. When seen in cross section (see FIGURE 31), the leaves often seem to have lacunae of epidermal cells, hairs, and stomata inside the mesophyll tissue, but actually such chambers are always connected with the outside. The stomata of these species are often limited to the lacunae. *Lyonia latifolia* var. *latifolia* (high-elevation forms) and *L. alpina* also rarely form such pockets.

The leaf venation pattern varies from brochidodromous (FIGURE 21) to eucamptodromous (FIGURE 24) or rarely more or less acrodromous (FIGURE 27, g) (see TABLE 8; Hickey, 1973; Dilcher, 1974; Melville, 1976). This character is often useful in identifying the Asian taxa. All species of sects. LYONIA and ARSENOCOCCUS have leaves with brochidodromous venation. The leaves of *L. lucida* are unique in having an intramarginal vein. Differences in the angle of divergence of the secondary veins and in their prominence and curvature near the margin are helpful in distinguishing taxa, especially in sect. PIERIDOPSIS (FIGURES 21–24, 27).

The third-order veins vary from reticulate to percurrent, with the former being the more common condition (TABLES 7, 8). *Lyonia buchii* and *L. heptamera* are unusual in that they are the only species of sect. LYONIA that often have percurrent tertiary veins. Percurrent veins are more common in *L. mariana, L. ligustrina,* and especially in sect. PIERIDOPSIS. They usually form an oblique angle with the midrib but often vary from parallel to perpendicular with it in different parts of the leaf.

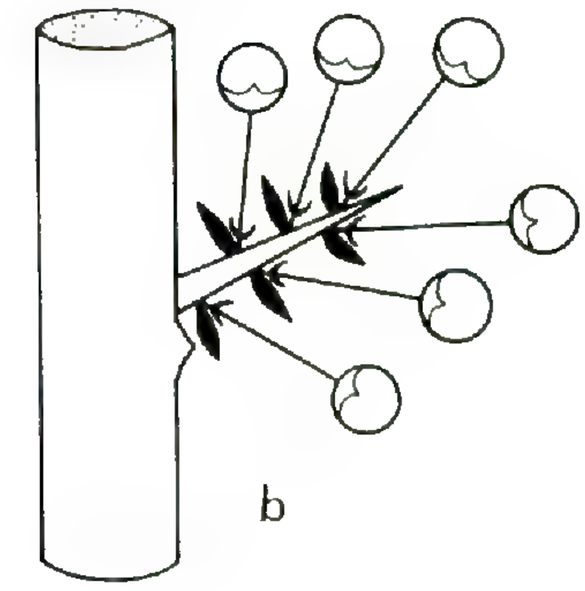
The higher-order veins are reticulate, the areoles are usually isodiametric in shape, and the vein endings simple or forked to dendroid (FIGURES 17, 18). The vein endings are surrounded by a sheath of lignified, isodiametric cells (see Lems, 1964) that stain darkly in sects. ARSENOCOCCUS and PIERIDOPSIS and in *L. mariana,* and that give the end a blunt appearance; they are usually difficult to see in sect. LYONIA (TABLE 8), so the end looks pointed. The ultimate veins of the generalized species of sect. LYONIA are often slender and tend to have blunt endings (FIGURE 17). However, the anatomically specialized *L. buchii* and *L. heptamera* also tend to have blunt vein endings.

The density of the ultimate venation and the size of the areoles is rather variable within the genus, but these characters have not been quantified. The areoles are especially small in *Lyonia macrocalyx* and in some varieties of *L. ovalifolia.* The morphologically specialized species of sect. LYONIA often have strongly thickened high-order veins (FIGURE 18). The areoles of such taxa in this group as *L. tuerckheimii* and *L. alainii* are rounded, while those of others such as *L. nipensis, L. obtusa,* and *L. macrophylla* are angular. It is of interest that the generalized species *L. affinis* has angular areoles, indicating a relationship to more specialized Cuban species (such as *L. obtusa*), while the generalized *L. rubiginosa* has more or less rounded areoles and is thus likely closer to *L. tuerckheimii.* In general, venation characters strongly reinforce the taxonomic groupings derived from a consideration of other criteria.

The adaxial leaf epidermis of some Caribbean species (e.g., *Lyonia glandulosa, L. urbaniana,* and *L. heptamera*) is often rough with the persistent bases of peltate scales, but in most species it is quite smooth, and lustrous or dull. *Lyonia ovalifolia* (sometimes), *L. villosa* (usually), and *L. macrocalyx* (always) have glaucous abaxial leaf surfaces.

INFLORESCENCES

The flowers of *Lyonia* are borne in axillary fascicles, racemes, or panicles on branches of the previous or (less commonly) the present season (see



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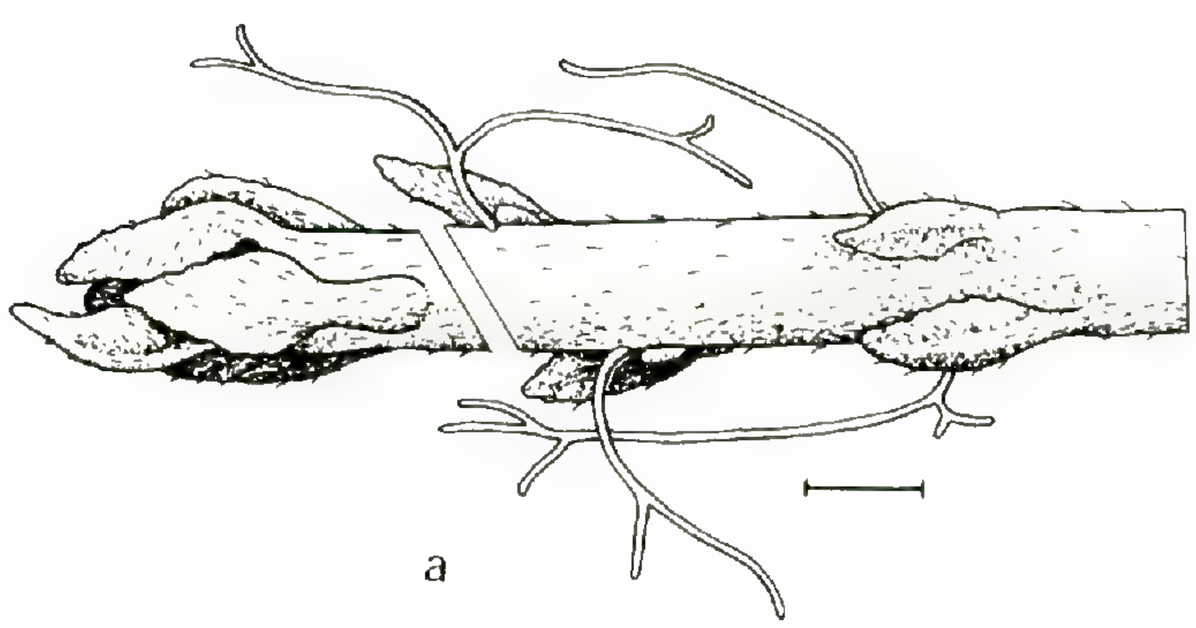

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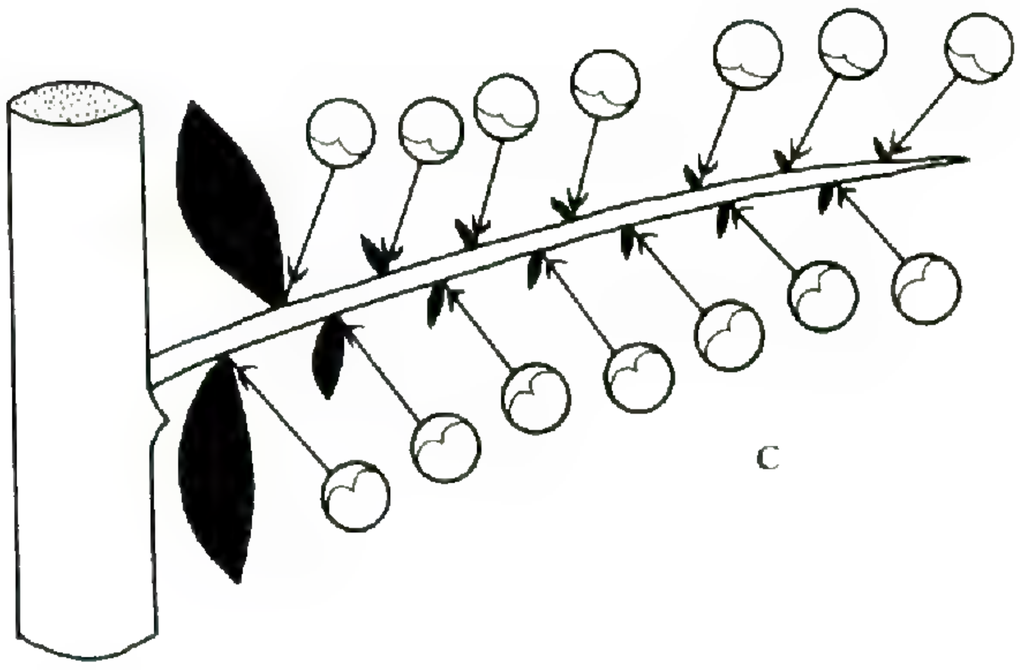

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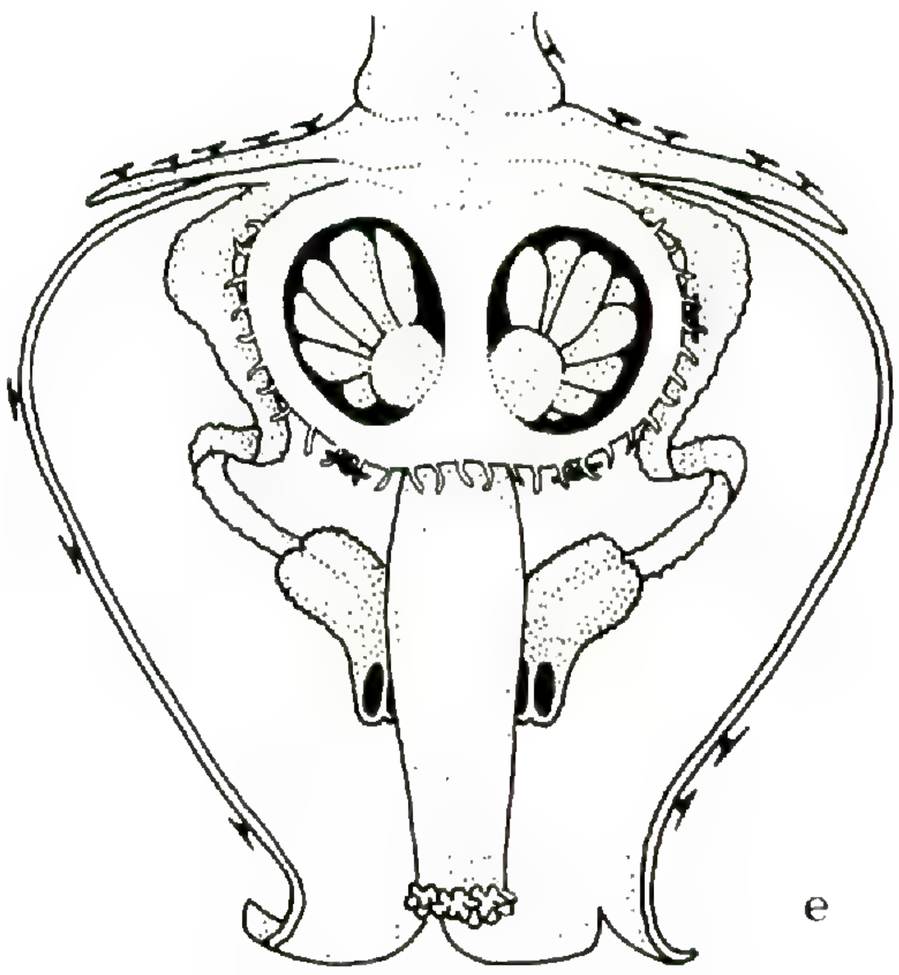

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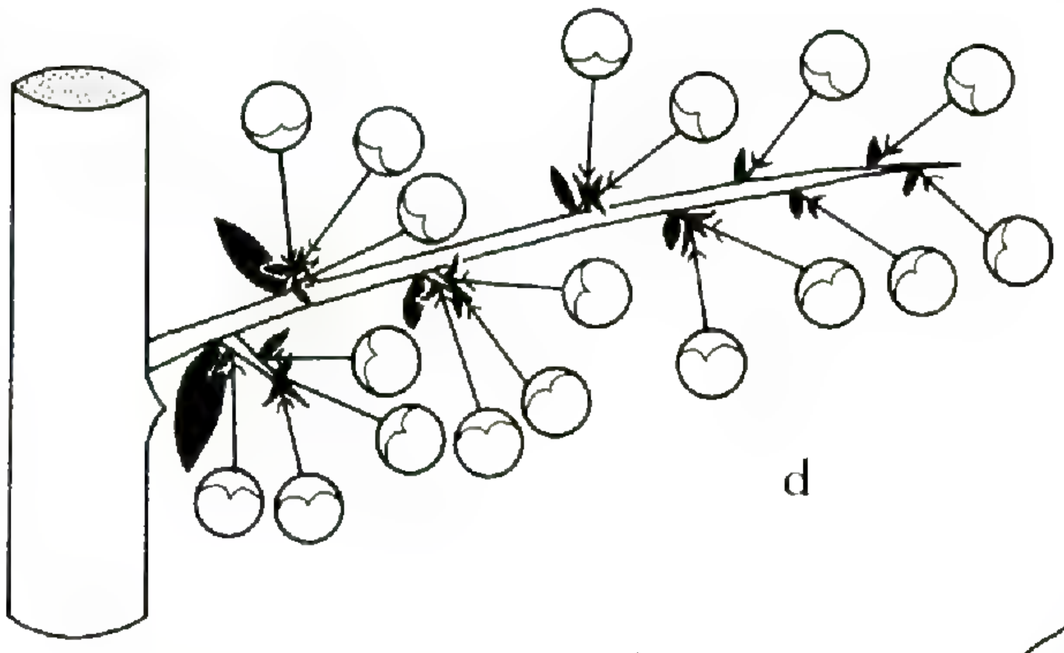

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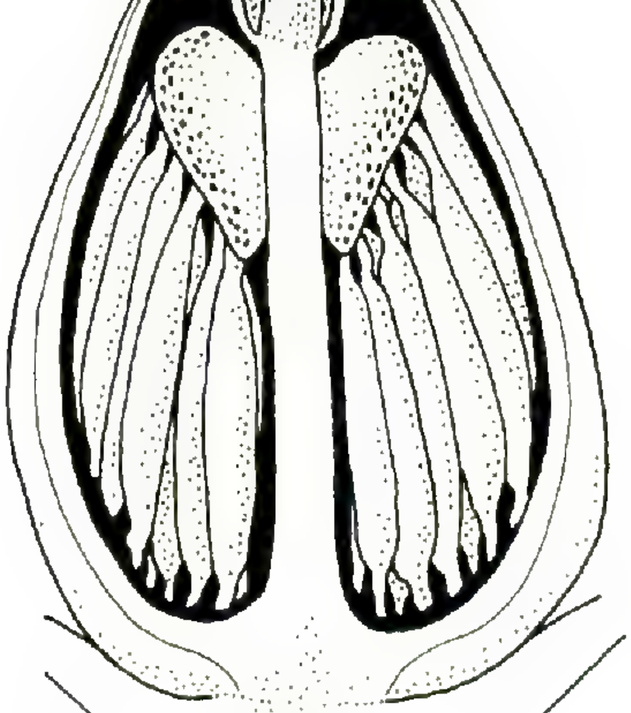

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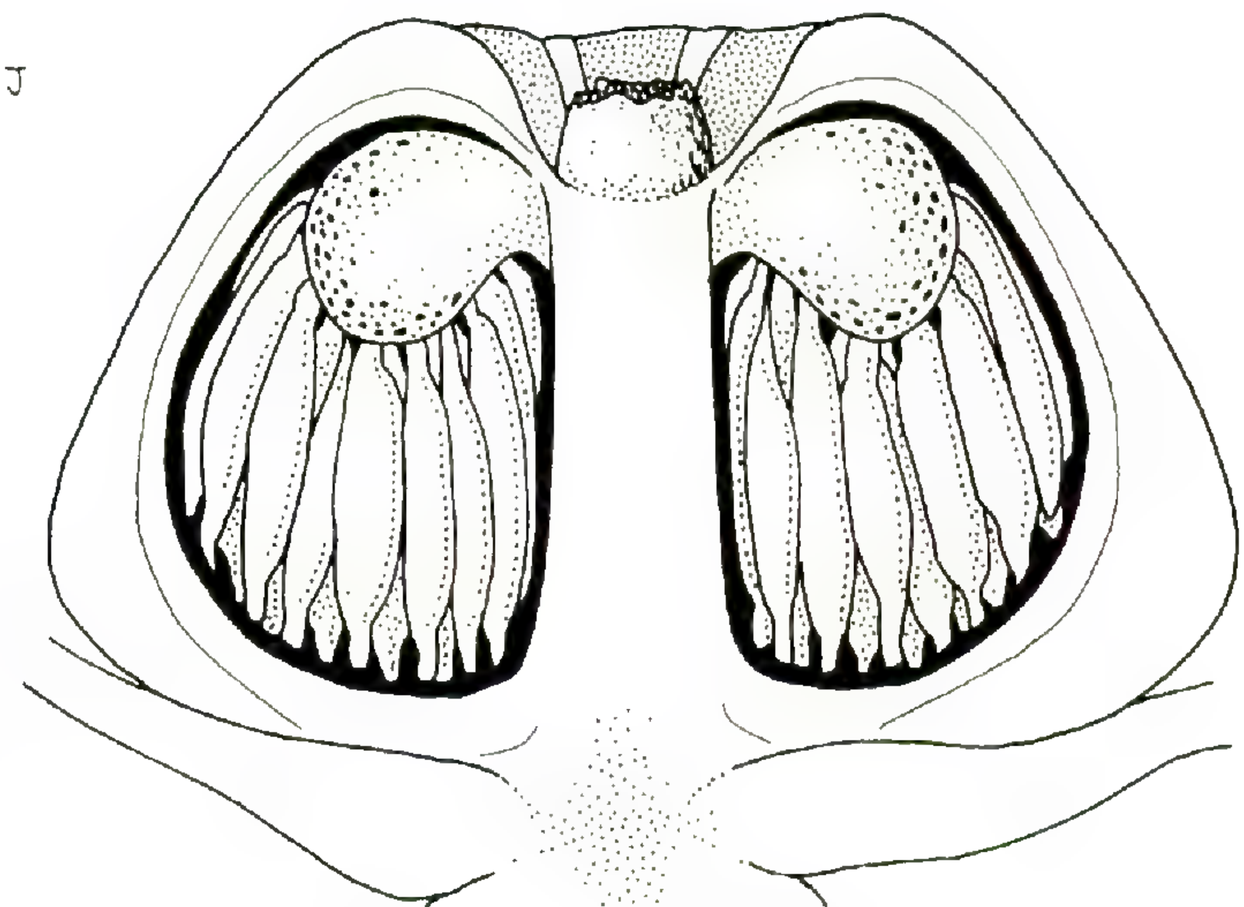

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FIGURE 11, and Lems, 1962). In *Lyonia* there is always one inflorescence per leaf axil. The species of sects. LYONIA and MARIA characteristically bear flowers in fascicles, although *L. heptamera, L. buchii,* and occasionally *L. fruticosa* and *L. tuerckheimii* have short racemes. All the species of sect. PIERIDOPSIS have racemes; in some species these reach 10–20 cm. in length. However, *L. villosa* often tends to have very short racemes, a trend that, if continued, would result in fascicles similar to those of sect. MARIA. The flowers are borne spirally on these horizontal to slightly ascending racemes, but since the flowers are pendulous, they make the racemes appear one sided or secund. In *L. compta,* the racemes are rigidly ascending, and the pendulous flowers are positioned on all sides. The inflorescence of *L. ligustrina* (sect. ARSENOCOCCUS) is the most complex of the genus; it is a raceme of fascicles or of short racemes (subpaniculate). Toward the apex of the inflorescence, the fascicles (or racemes) become progressively reduced, and near the end they are often represented by only solitary flowers (FIGURE 11). There are no terminal flowers in any of these inflorescence types; the apex of the raceme or fascicle simply aborts. They are thus polytelic (see Weberling, 1965). The fascicles occurring in sect. MARIA and in most of the species of sect. LYONIA are probably derived from racemes through a shortening of the inflorescence axis. *Lyonia ligustrina,* with its complex, subpaniculate inflorescence, may also have evolved from ancestors with racemose inflorescences through compression of the morphological structures of two growing seasons into one, or by reduction of a paniculate inflorescence.

The primitive inflorescence type in *Lyonia* is thus possibly a raceme, although it is likely that this is not primitive within the Ericaceae as a whole. According to Weberling (1965), the polytelic inflorescence type is more highly evolved than the monotelic type. Within the Andromedeae, only *Craibiodendron* has inflorescences with terminal flowers; thus, the inflorescence of *Craibiodendron,* a large panicle, is possibly primitive within the tribe.

MORPHOGENETIC CYCLE

As in most other members of the Andromedeae, the shoot meristem in *Lyonia* has a limited life span, and growth in height is achieved by a succession of lateral buds rather than by continuous growth of a terminal meristem (see Lems, 1962). In *Lyonia* a vegetative branch, which has vegetative and floral buds variously arranged, is formed in the spring and early summer. In sects. MARIA and ARSENOCOCCUS the floral buds are usually above the vegetative ones; in species of sect. PIERIDOPSIS except *L. compta,* they are usually below; and in sect. LYONIA the two are often somewhat intermixed, although the floral buds are usually borne toward the apex of the shoot.

FIGURE 11. a, horizontal underground rhizome of *Lyonia ligustrina* var. *ligustrina* (scale = 1 mm.). b–d, diagrammatic inflorescences: b, *Lyonia* sects. LYONIA and MARIA; c, *Lyonia* sect. PIERIDOPSIS; d, *Lyonia* sect. ARSENOCOCCUS. e, diagrammatic longitudinal section of flower of *L. fruticosa*. f, g, longitudinal sections of capsules, × 7.5: f, *L. ferruginea;* g, *L. heptamera.*

Each floral bud contains an embryonic inflorescence in which the individual flowers are as yet incompletely differentiated. No pollen or ovules can be distinguished before winter. In the spring these buds open, the inflorescence emerges, and the flowers mature; meiosis thus occurs in the spring. At this time, or soon after, the vegetative buds open and new vegetative shoots that continue the cycle begin to grow. Fruit maturation occurs during the summer, and the seeds are mature by fall. The capsules are persistent, and the seeds are dispersed throughout the winter and the following spring and summer. In sect. LYONIA periodicity of growth is less clear, as might be expected in plants from tropical or subtropical climates, and *L. heptamera* and *L. buchii* branch and flower almost continually. *Lyonia fruticosa* is unusual in that its inflorescences and flowers are formed mainly on the shoots of the present season (although some flowers are usually also produced on branches of the previous year). As the shoots grow out in the spring, some of their axillary buds immediately develop inflorescences; thus, flowering occurs soon after the young shoots are produced (from spring to summer). Dormancy of floral buds in some temperate species such as *L. mariana* and *L. ovalifolia* is often prematurely broken, and occasional plants can be found in flower in the autumn.

FLORAL BRACTS AND BRACTEOLES

In all species of *Lyonia,* the pedicel is subtended by a single bract. The size of this bract varies from only 2–3 mm. long to large (ca. 11 cm.) and foliaceous. In sects. LYONIA and MARIA the bracts are usually all very small and caducous or deciduous, but in sects. ARSENOCOCCUS and PIERIDOPSIS they vary from minute and caducous (near the apex of the inflorescence) to foliaceous and persistent (toward the base). The size, number, and position of these foliaceous bracts is helpful in differentiating the varieties of *L. ovalifolia* and *L. ligustrina,* and in separating *L. compta* from the remaining Asian species.

Each pedicel in *Lyonia* has a pair of bracteoles. They are usually located at or near the base of the pedicel and are characteristically minute, linear to triangular (or, less commonly, ovate), and less than 1 to (at most) 6 (e.g., *Lyonia heptamera* and *L. macrocalyx*) mm. long. The bracteoles are opposite and at the base of the pedicel in sects. PIERIDOPSIS, ARSENOCOCCUS, and MARIA, while in sect. LYONIA they vary from opposite and basal to (in a few species) often alternate and on the lower fifth of the pedicel. The bracteoles are often caducous in sects. LYONIA, PIERIDOPSIS, and ARSENOCOCCUS but are usually persistent in sect. MARIA. The size, shape, and position of the bracteoles are, in general, too uniform to be useful at the specific level.

FLOWERS

All species have actinomorphic, perfect, pendulous flowers, although the pedicel curves upward as the fruits begin to develop, ultimately placing the capsules in an erect position. The flowers of most species are five-merous, but in a few (e.g., *L. heptamera* and *L. buchii*) they are consistently six- or seven-merous, and in several others (see keys) they are usually four-merous.

This latter character has evidently evolved several times because species with four-merous flowers are independently related to species with five-merous ones. In some predominantly five-merous species (e.g., *L. rubiginosa, L. latifolia,* and *L. urbaniana*), individuals with a mixture of five- and four-merous, or all four-merous, flowers are found; occasionally the reverse occurs (as in *L. myrtilloides*). *Lyonia fruticosa* usually has five-merous flowers, but individuals with a mixture of five-, six-, and seven-merous ones can often be found. Thus, numerical variation—although a useful taxonomic character—must be used with care.

PEDICEL. The pedicel varies in length from only 1.5–4.5 mm., as in *Lyonia octandra* and *L. trinidadensis,* often up to 20–30 mm., as in *L. obtusa* and *L. nipensis.* Pedicel length is not a very useful taxonomic character, since the pedicel tends to elongate as the flower and fruit develop. Nearly all species have a clearly developed articulation (or at least a slight constriction) between the pedicel and the calyx, but in *L. glandulosa* and *L. toaënsis* the pedicel and calyx join smoothly.

CALYX. The calyx is composed of four to seven (or rarely eight) sepals that are connate only at the very base. The calyx lobes can be glabrous to densely pubescent or lepidote, and they are usually persistent, except in *Lyonia mariana* (and sometimes in *L. macrocalyx*), in which they fall with the leaves. (*Lyonia macrocalyx* is also unusual in that it has expanded and subfoliaceous lobes, which may be variously notched at the apex.) Stomata are usually present only on the abaxial surface. The lobes show a marked interspecific variation in length (for example, 0.5–1.5 mm. in *L. ligustrina* and 4.5–9(–11) mm. in *L. macrocalyx*). They are valvate in the buds of sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS, but are slightly imbricate in sect. LYONIA. In some taxa (e.g., *L. lucida* and *L. mariana*) they are slightly swollen near the base. The apex varies from acuminate to acute, obtuse, or rounded, but is usually acute to acuminate in sect. LYONIA.

COROLLA. The corolla is always sympetalous and deciduous. It is usually thin and delicate, except in *Lyonia heptamera, L. buchii, L. nipensis, L. obtusa,* and *L. latifolia,* where it is rigid and fleshy. Stomata are nearly always present on the outer surface but lacking on the inner. The corolla varies in shape from cylindrical to elongate-urceolate, shortly urceolate, globose, or more or less campanulate, with four to seven (or rarely eight) usually short, imbricate lobes. *Lyonia buchii* is unusual in having well-developed corolla lobes, often 4 mm. long, and *L. lucida* is unique in that its corolla is cylindrical with a swollen base. The corolla is most often white, or white with a pinkish tinge toward the mouth, but occasional pink forms occur. *Lyonia lucida* characteristically has pink (to even reddish) corollas. The size of the corolla varies considerably, from 2–3 mm. long and 1–2.2 mm. wide in *L. glandulosa* to 8–13 mm. long and 8–13 mm. wide in *L. heptamera.* The shape, size, and color of the corolla are all useful taxonomic criteria in *Lyonia* (see keys for examples).

The multicellular hairs that characterize each section also occur on the

outside of the corolla, and the density of these hairs is useful in distinguishing a few Cuban species such as *Lyonia latifolia* and *L. nipensis.* Very rarely, there are also a few unicellular hairs on the outside of the corolla; these are most common in the western populations of *L. mariana.* The inner surface is always completely glabrous.

ANDROECIUM. The flowers of all species of *Lyonia* have twice as many stamens as corolla lobes (i.e., 8 to 14, rarely 16). They are arranged in two whorls that occasionally differ slightly in size, and are inserted at the base of the corolla; the outer whorl is opposite the corolla lobes. The stamens are always included and are arranged in a tight ring, with the anther pores facing inward and pressed against the style (FIGURE 11). (In addition, they show the peculiar characters of the ericaceous stamen—see Artopoeus, 1903; Matthews & Knox, 1926). The filaments are slender, flattened, geniculate, and slightly to markedly swollen near the base. They are roughened in all species of sect. LYONIA and in *L. lucida,* but in *L. ligustrina, L. mariana,* and most species of sect. PIERIDOPSIS, they have long, unicellular hairs, at least near the base. *Lyonia chapaënsis* is unusual in that its filaments sometimes lack unicellular hairs and are papillose. *Lyonia villosa* very rarely has a few large, multicellular hairs on the filaments (FIGURE 9). Filament length varies from only 1–1.5 mm. in *L. glandulosa* to as long as 9 mm. in *L. ovalifolia;* it is strongly correlated with flower size.

A pair of spurs is present near the apex of the filament in many species of all four sections of the genus, although those of species such as *Lyonia ligustrina* are minute and often overlooked. The presence of filament spurs is a character that is taxonomically useful in distinguishing a few Asian species, although it must be used with caution since some species vary infraspecifically in this character. The position at which the spurs are borne is also quite variable: they can occur on the upper portion of the filament to just below the anther-filament junction, but they are never on the back of the anther itself (FIGURES 20, 22, 24, 25, 29, 30, 34, 49). All species have disintegration tissue that breaks down as the stamen matures to produce a white, powdery substance (Palser, 1951) on the back of each anther lobe, extending at least along the apex of the filament and along the upper edge of the spurs (when these are present). The anthers are papillose (especially toward the base), have four microsporangia, and open by two introrse-terminal (but morphologically basal) elliptic pores. The anthers lack apical awns but are slightly apiculate. These apiculae seem to be formed during the dehiscence of the anther and are not present as identifiable structures before this process.

GYNOECIUM. The stigma is truncate to capitate, obscurely four- to seven-(or eight-)lobed, and minutely papillose. The lobes are alternate with the loculi of the ovary. The style is columnar, glabrous, straight, and with a four- to seven- (or eight-)fluted central canal; it is impressed into the apex of the ovary. The length of the style is strongly correlated with the size of the corolla and has thus not been used taxonomically. A swelling near the base of the style may be developed in many taxa; it may be of taxonomic importance, but further investigations are needed since it is difficult to observe

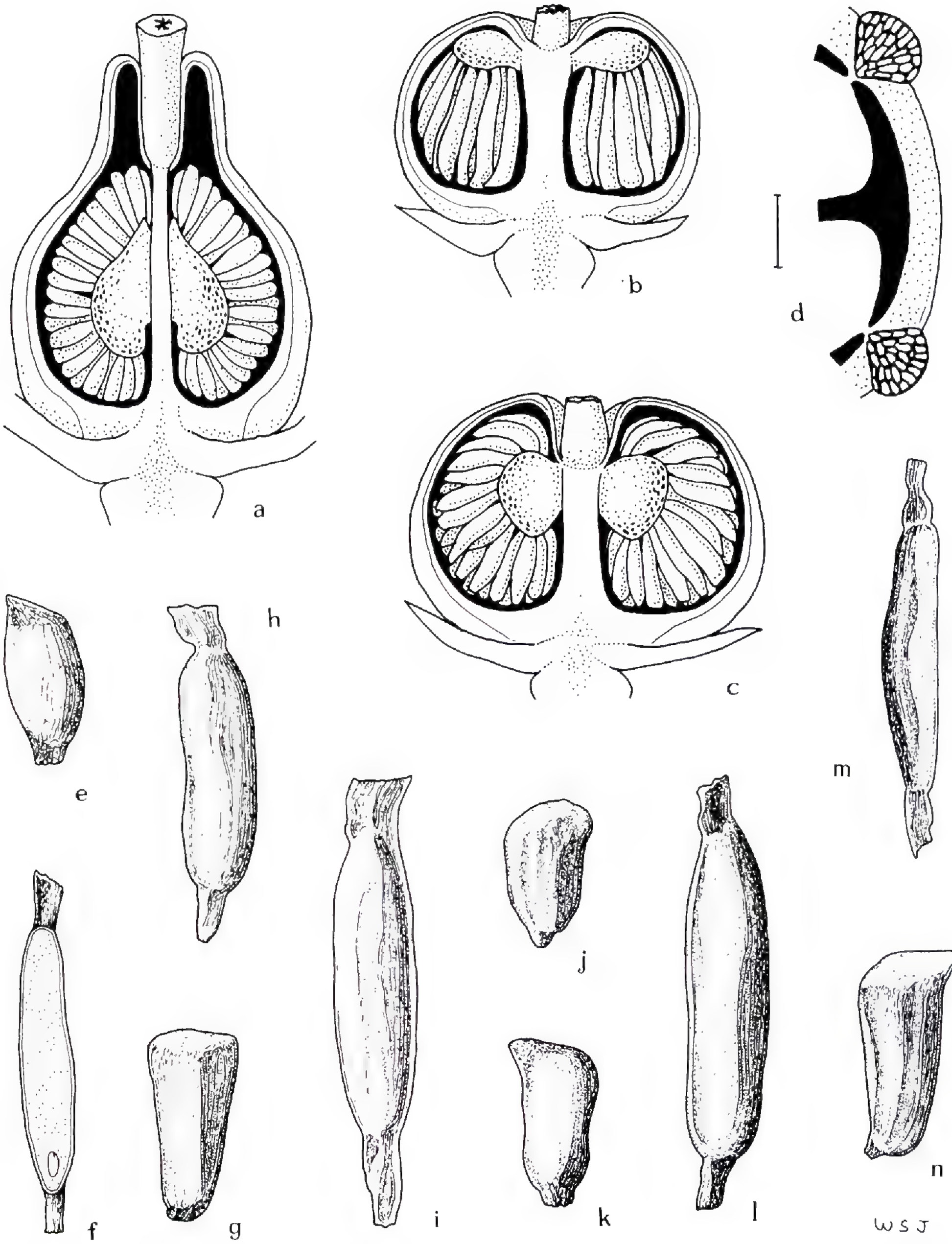


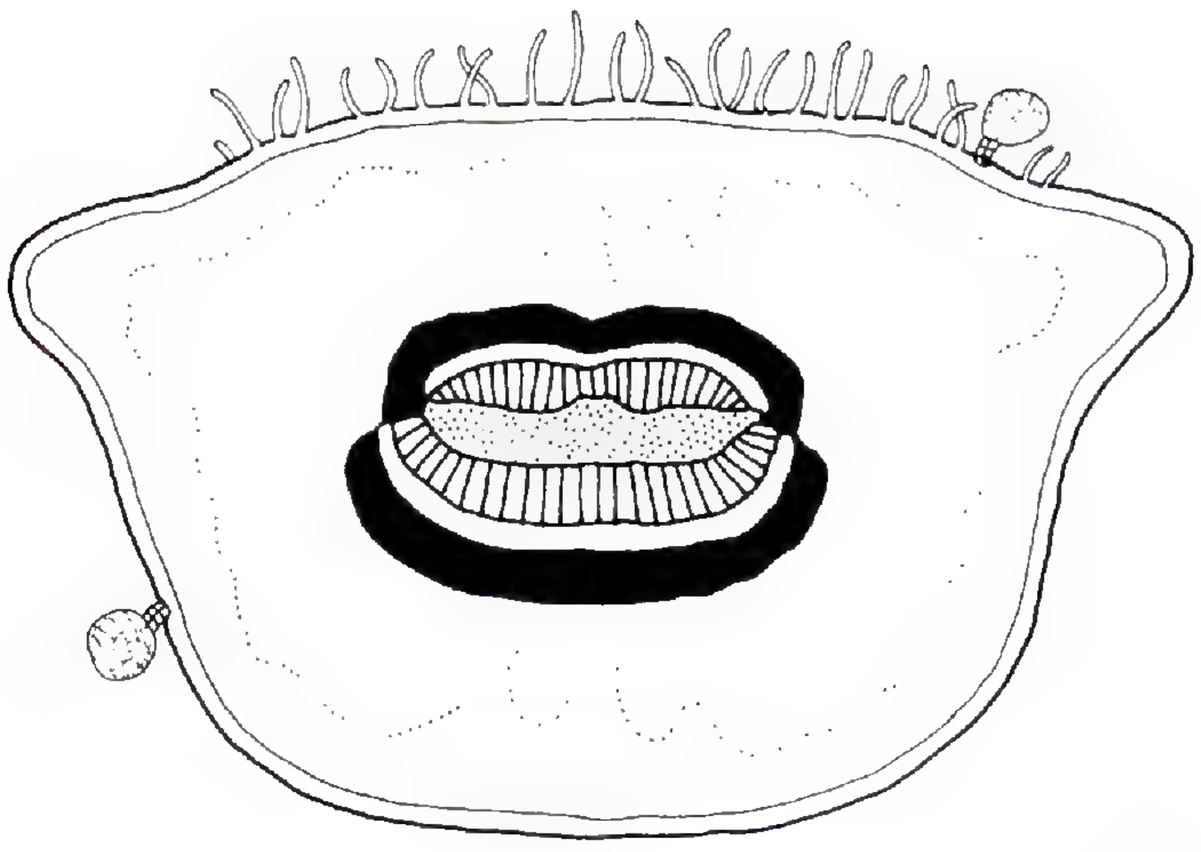
FIGURE 12. Fruits and seeds of *Lyonia*. a–d, capsules. a–c, longitudinal sections, × 7.5: a, *L. mariana;* b, *L. ligustrina;* c, *L. ovalifolia* var. *ovalifolia.* d, *L. mariana,* cross section of single valve and two adjacent sutures (scale = 0.5 mm.). e–n, seeds, × 20: e, *L. ovalifolia* var. *ovalifolia;* f, *L. fruticosa,* longitudinal section showing embryo and endosperm; g, *L. mariana;* h, *L. tuerckheimii;* i, *L. heptamera;* j, *L. lucida;* k, *L. villosa* var. *sphaerantha;* l, *L. nipensis* var. *nipensis;* m, *L. fruticosa;* n, *L. ligustrina* var. *ligustrina.*

TABLE 6. **Chromosome numbers of Lyonia.**

SPECIES	*n*	COLLECTION	LOCALITY
L. truncata var. *montecristina*	12	*Judd 1341* (A)	Dominican Republic, Cordillera Central, S. of El Rubio, ca. 640 m.
L. truncata var. *truncata*	12	*Judd 1478* (A)	Dominican Republic, Sierra de Baoruco, S. of Aceitillar, ca. 1000 m.
L. heptamera	12	*Judd 1214* (A)	Dominican Republic, Cordillera Central, near Valle Nuevo, ca. 2150 m.
L. octandra	12	*Judd 658* (A)	Jamaica, near Blue Mountain Peak, ca. 2130 m.
L. fruticosa	12	*Judd 1963* (A)	Greenhouse plant, originally collected in Long Co., Georgia (*Judd 325*)
L. ligustrina var. *ligustrina*	12	*Judd 1663* (A)	Massachusetts, Ponkapoag Bog, Canton, Middlesex Co.

in dried material. The ovary is superior, four- to seven- (or eight-)locular, and glabrous to densely covered with unicellular hairs, peltate scales, or glandular hairs. The placentae are axile and are borne subapically to nearly "basally" on a central columella. Species with nearly basal placentae have very deeply impressed styles; the placentae are thus still apical with regard to the position of the junction between the style and ovary (FIGURES 11, 12). The placentae are very slightly bilobed and bear numerous anatropous ovules. The ovules have a single integument and a single-layered, evanescent nucellus; the gametophyte development is of the Polygonum type (see Palser, 1952). The species of sect. LYONIA have fewer ovules (and seeds) per locule than do those of the remaining sections. The shape of the ovary varies from

FIGURE 13. Petioles and pith cells of *Lyonia.* a–e, cross sections of petioles, × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, parenchyma cells with stipples). a, *L. mariana,* upper petiole. b, c, *L. lucida:* b, near base of petiole; c, upper petiole. d, *L. ferruginea,* mid-petiole. e, *L. macrophylla,* upper petiole. f, g, diagrammatic representations of pith cells from branches (greatly enlarged): f, homogeneous (*L. truncata*); g, heterogeneous (*L. ligustrina*).



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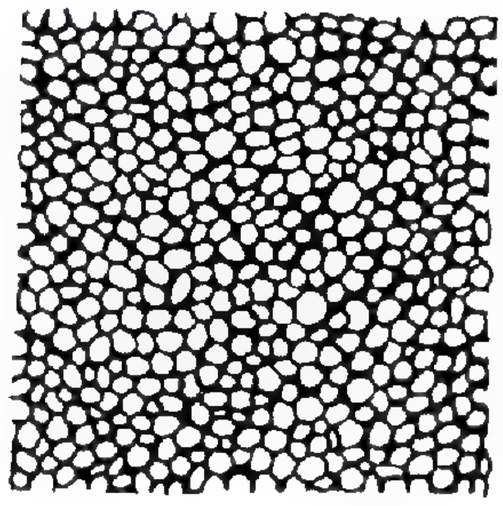

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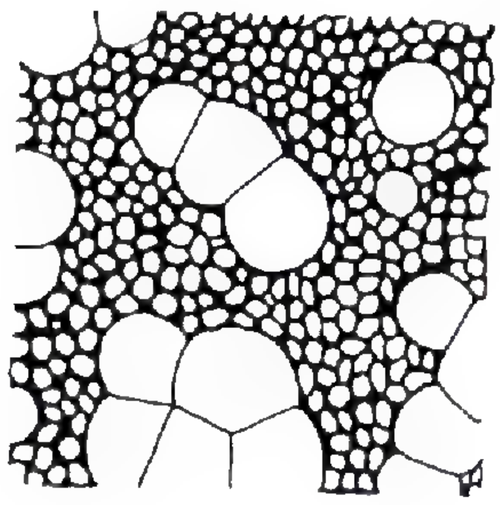

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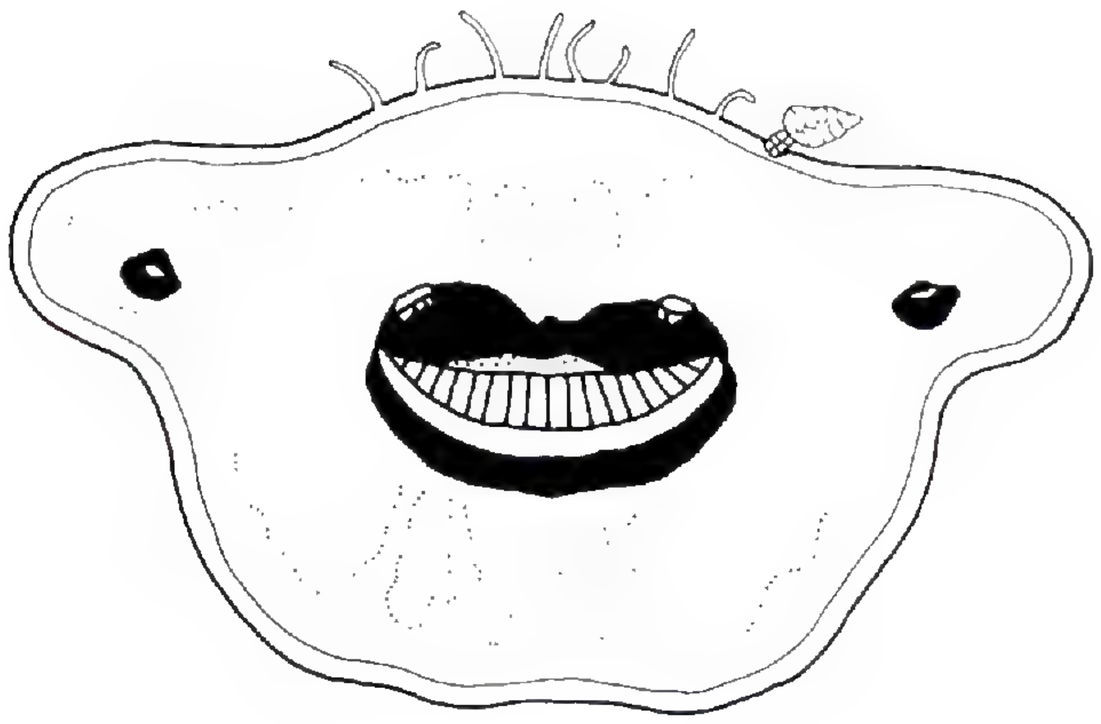

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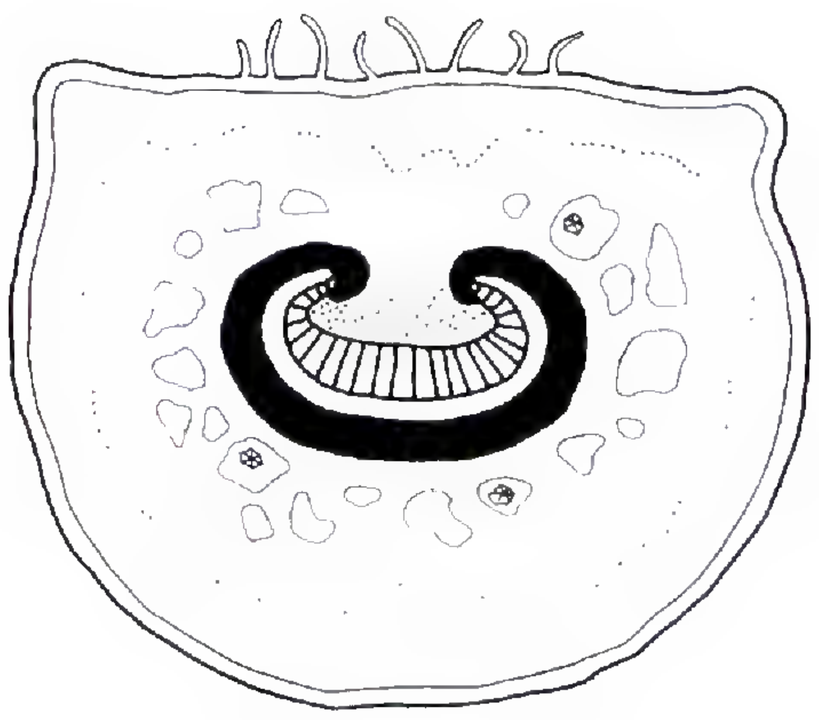

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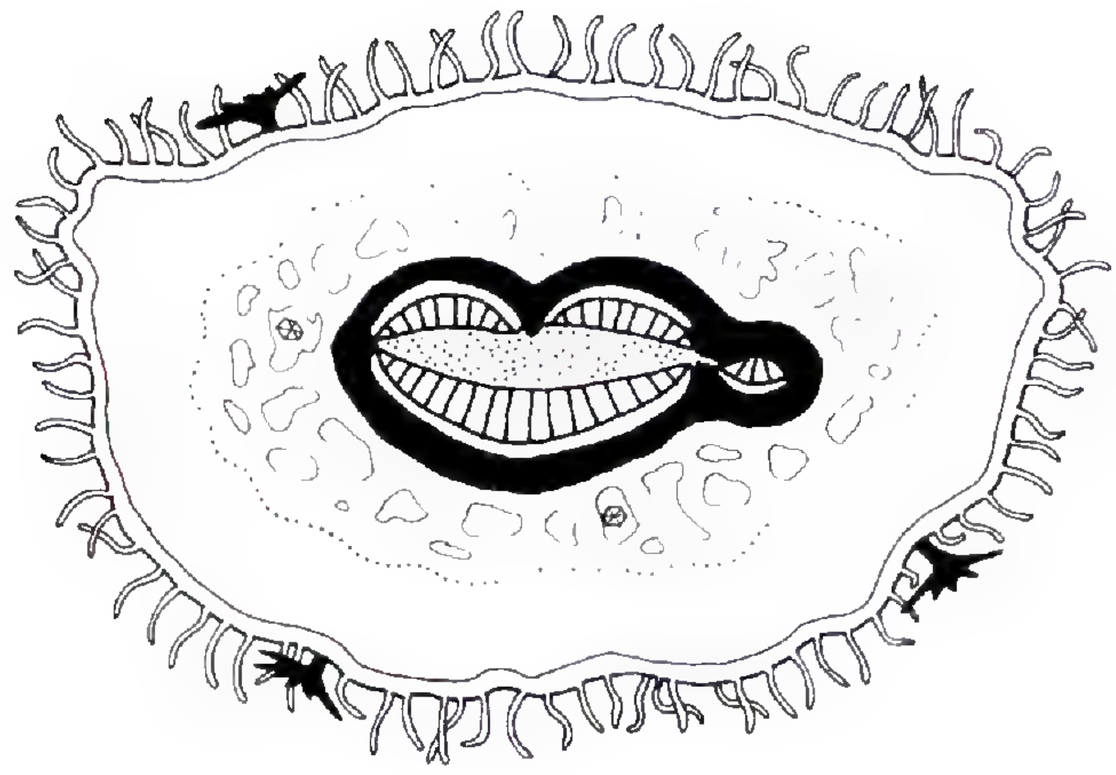

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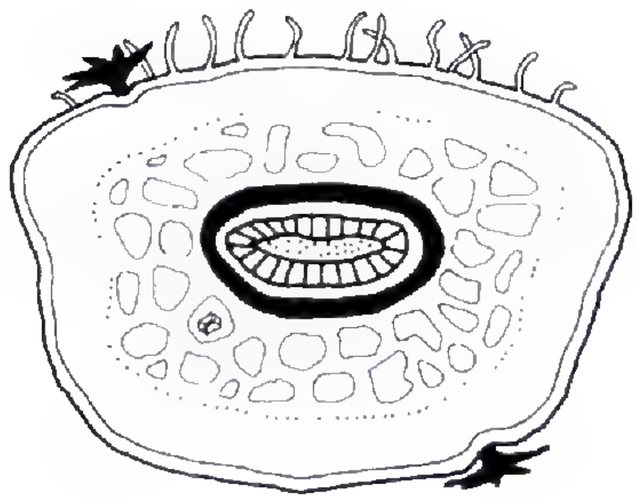

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TABLE 7. **Key to symbols and character abbreviations used in Table 8.**

SYMBOL	CHARACTER	ABBREVIATION	MEANING
A	Pith type (stem)	+	Heterogeneous
		–	Homogeneous
B	Lignification of leaf epidermis	I	Inner periclinal walls lignified but not strongly thickened
		II	Inner periclinal walls lignified and strongly thickened
		–	Not lignified, or only slightly lignified over major veins
C	Height : breadth ratio of adaxial leaf epidermal cells	Ratio	
D	Leaves with adaxial hypodermis of at least 1 cell layer	+	Yes
		(+)	Sometimes (or partial hypodermis)
		–	No
E	Adaxial hypodermis of 2 cell layers	+	Yes
		(+)	Partial
		–	No
F	Vascular bundle of petiole	I	Bifacial, usually forming cylinder
		II	Bifacial, forming cylinder including medullary bundles
		III	Bifacial, usually not joining to form cylinder
		IV	Unifacial
G	Veins of abaxial leaf surface forming raised-reticulate pattern	+	Yes
		–	No
H	Leaves usually with dense layer of unicellular hairs on abaxial surface	+	Yes
		–	No
I	Leaves papillose on abaxial surface	+	Yes
		–	No
J	Type of multicellular hairs	I	Peltate scales
		II	Short-headed hairs
		III	Long-headed hairs

TABLE 7 (*continued*).

SYMBOL	CHARACTER	ABBREVIATION	MEANING
K	Peltate scales sunken into abaxial leaf epidermis	+	Yes
		–	No
L	Pattern of lignified cells surrounding major leaf veins	I	Transcurrent veins
		II	Semitranscurrent veins
		III	Embedded veins
M	Pattern of major secondary leaf veins	+	Brochidodromous
		–	Eucamptodromous
		*	Extending to intramarginal vein
N	Pattern of 3° veins	+	Reticulate
		–	Percurrent
O	Vein endings	I	Surrounded by prominently staining cluster of lignified cells (thus appearing blunt)
		II	Not surrounded by prominently staining cells (thus appearing pointed)
P	Mesophyll tissue of leaves	+	1 or 2 layers of spongy cells lignified near abaxial epidermis
		–	Cells not lignified

ovoid to globose or subglobose, but this variation is better expressed in the mature fruit. A nectariferous disc is variously developed around the base of the ovary. A few stomata are often present.

FRUITS AND SEEDS

The fruit of *Lyonia* is a four- to seven- (or eight-)angled, subglobose, globose, narrowly to widely ovoid, ellipsoid, or urn-shaped, loculicidal capsule, with prominent, pale, thickened sutures that often separate from the adjacent valves in dehiscence (FIGURES 29, 34, 46, 48, 49). These thickened sutures are formed from a band of lignified cells running down the middle of the outside carpel wall (FIGURE 12) and are best developed in sect. LYONIA. The capsules of *Lyonia*, with their prominent sutures, are unique within the Ericaceae. *Lyonia compta* and *L. chapaënsis* are unusual in that they lack (or very nearly lack) these peculiar structures.

The size and shape of the capsules tend to be rather constant within a

TABLE 8. **Variation of selected anatomical and indumentum characters in Lyonia.***

TAXON (SPECIES NUMBER)	CHARACTER CODE A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1	-	-	±1	+	-	III	-	-	-	III	NA	III	+	+,-	I	-
2	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+,-	+,-	I	-
3A	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+	-	I	-
3B	-	-	.5-1	-	-	III	-	-	-	III	NA	III	+	-	I	-
3C	-	-	.5-1	-	-	I, III	-	-	+	III	NA	III	+	-	I	-
3D	-	-	.5-1	-	-	I, III	-	-	+,-	III	NA	III	- (+)	-	I	-
3E	-	-	.3-.5	-	-	III	-	-	-	III	NA	III	-	+,-	I	+
3F	-	-	.5-1	-	-	III	-	-	-	III	NA	III	-	-	I	+
3G	-	-	1-2	-	-	I, III	-	-	-	III	NA	III	-	+,-	I	+
4A	-	-	.5-1	-	-	III	-	-	+	III	NA	III	+	-	I	-
4B	-	-	±1	-	-	III	-	-	+	III	NA	III	+	-	I	-
4C	-	-	.5-1	-	-	III	-	-	- (+)	III	NA	III	+	-	I	-
5	-	-	.5-1	-	-	III	-	-	+	III	NA	III	+,-	+,-	I	-
6A	+	-	.3-1	-	-	III	-	-	-	III	NA	III	+	+,-	I	-
6B	+	-	.3-1	-	-	I, III	-	-	-	III	NA	III	+	+,-	I	-
7	-	-	.5-1	-	-	I, III	-	-	-	II	NA	III	+,-	+,-	I	-
8	-	II	.5-1	-	-	III, IV	-	-	-	II	NA	III	* (-)	+	II	-
9	-	I	±1	+	(+)	II	+	+	-	I	-	II	+	+,-	II	-
10	-	I	1-1.5	+	-	II	+	+	-	I	-	II	+	+,-	II	-
11	-	I	1-2	+	-	I	+	+	-	I	-	I	+	+	II	-
12	-	I	1-3	+	-	I	+	+	-	I	-	I	+	+	II	-
13	-	I	.5-2	+	-	1	+	+	-	I	-	I	+	+	II	-
14	-	I	1-2	+	+ (-)	I	- (+)	+	-	I	+,-	I	+	+	II	-
15A	-	I	1-1.5	+	-	I	-	+	-	I	+	I	+	+	II	-
15B	-	I	.5-2	+	-	I	-	+	-	I	+	I	+	+	II	-
16	-	II	.5-3	(+)	-	I	-	-	-	I	+	I	+	+	II	-
17	-	I	1-1.5	+	+	I	-	-	-	I	+	I	+	+	II	-
18A	-	I	.5-1	+	-	I	-	-	-	I	+	I	+	+	II	-
18B	-	I	.5-1	+	-	I	-	-	-	I	+	I	+	+	II	-
18C	-	I	.5-1.5	(+)	-	I	-	-,+	-	I	+	I	+	+	II	-
19	-	II?	.5-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-

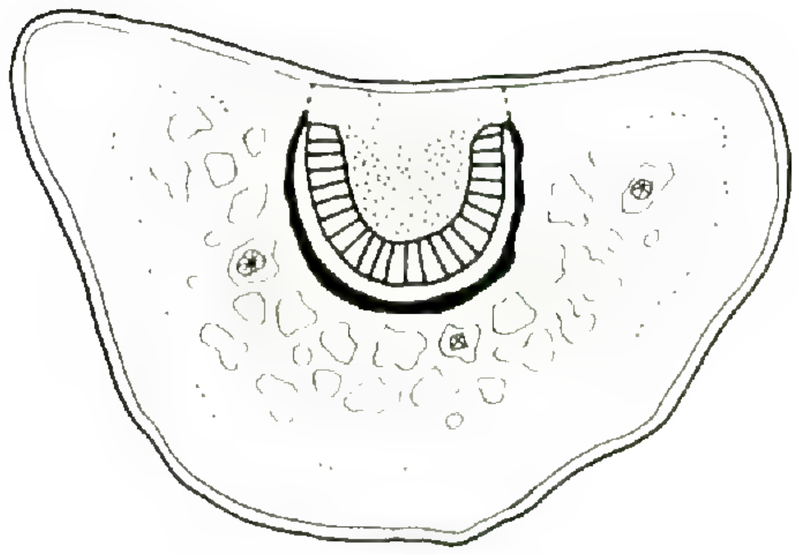
TABLE 8 (*continued*).

TAXON (SPECIES NUMBER)	CHARACTER CODE A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
20	-	II?	5-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-
21	-	I	.5-1	(+)	-	I	-	-	-	I	+	I	+	+	II	-
22	-	II	.5-1	+	-	I	-	+	-	I	+	I	+	+	II	-
23	-	II	.5-1	(+)	-	I	-	+	-	I	+	I	+	+	II	-
24A	-	II	2-4	(+)	-	I	-	+	-	I	-	I	+	+	II	-
24B	-	II	1-1.5	-	-	I	-	+	-	I	-	III	+	+	II	-
25A	-	II	1-2.5	-	-	I	-	-	-	I	+	III	+	+	II	-
25B	-	II	1-2	-	-	I	-	-	-	I	+	III	+	+	II	-
26	-	II	1-3	-	-	I	-	-	-	I	+	I	+	+	II	-
27	-	II	1-2	+	-	I	-	-	-	I	+	I	+	+	II	-
28	-	II	1-1.5	+	-	I	-	-	-	I	+	I	+	+	II	-
29	-	I	.3-1	-	-	I	-	-	-	I	+	I	+	+	II	-
30A	-	I	±1	+	(+)	I	- (+)	+	-	I	+	I	+	+	II	-
30B	-	I	±1	+	-	I	-	+	-	I	+	I	+	+	II	-
32A	-	II	±1	+	-	I	-	+	-	I	+	I	+	+	II	-
32B	-	II	±1	(+)	-	I	-	+	-	I	+	III, I	+	+	II	-
33	-	I	±1	-	-	I	-	- (+)	-	I	+	III, I	+	+	II	-
34	-	I	±1	-	-	I	-	+	-	I	+	III	+	+	II	-
35	-	I	.5-1	(+)	-	I	-	+	-	I	+	III	+	+	II	-

*For explanation of symbols and character abbreviations, see TABLE 7.

species but often differ greatly between species (FIGURES 28, 29, 34, 38, 41, 52, 56); these differences are very useful in identification. The shape of the capsule is useful in distinguishing among the varieties of *Lyonia ovalifolia* and of *L. villosa*. Other interesting variations in the shape and size of the capsules are evident in the keys.

The seeds are minute, brown, oblong-ovoid to linear or spindle shaped, with the ends drawn into short, sterile extensions or "tails" (in sect. LYONIA; FIGURE 12) or with one end more or less truncated (in sects. MARIA, PIERIDOPSIS, and ARSENOCOCCUS; FIGURE 12). They are never winged and have a loose, thin testa composed of a single layer of very much elongated cells. The seed morphology is too uniform to be very useful in identifying species in *Lyonia*.



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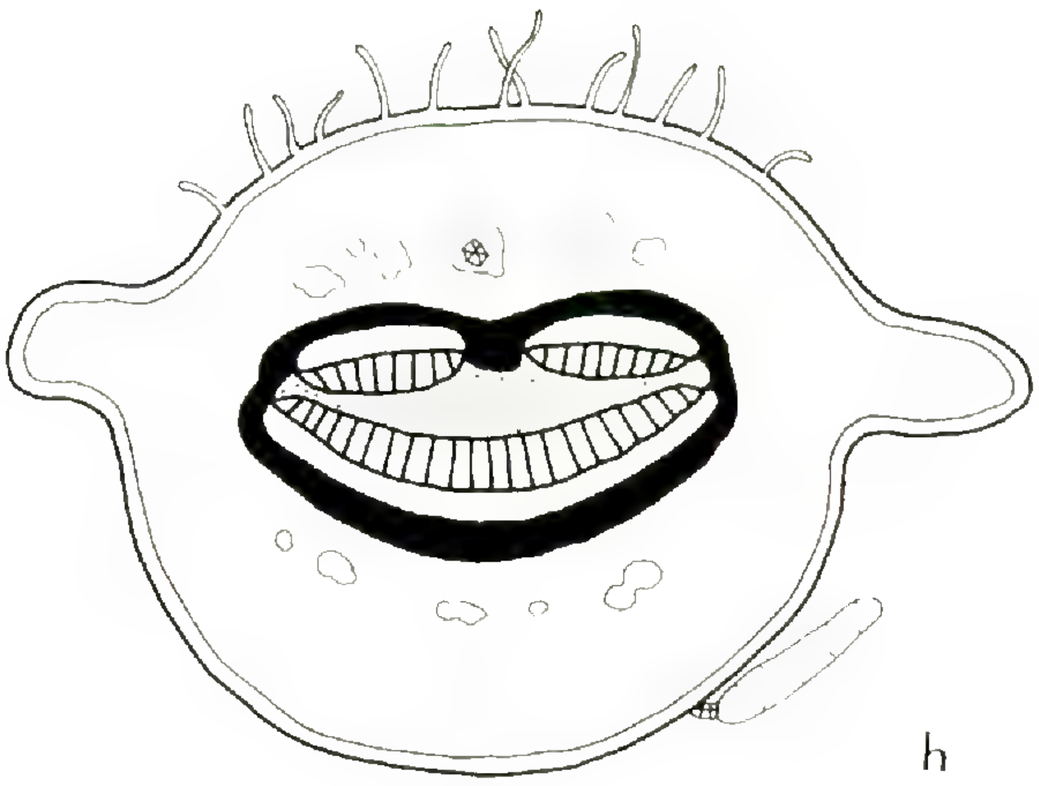

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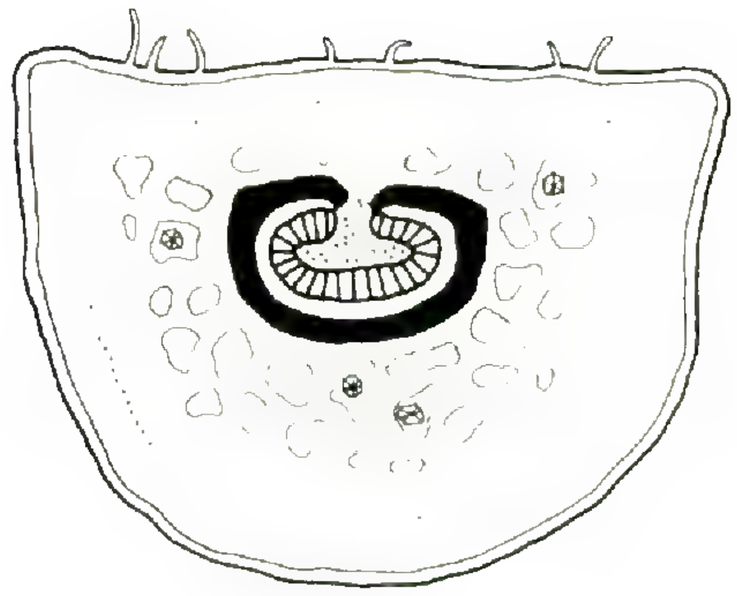

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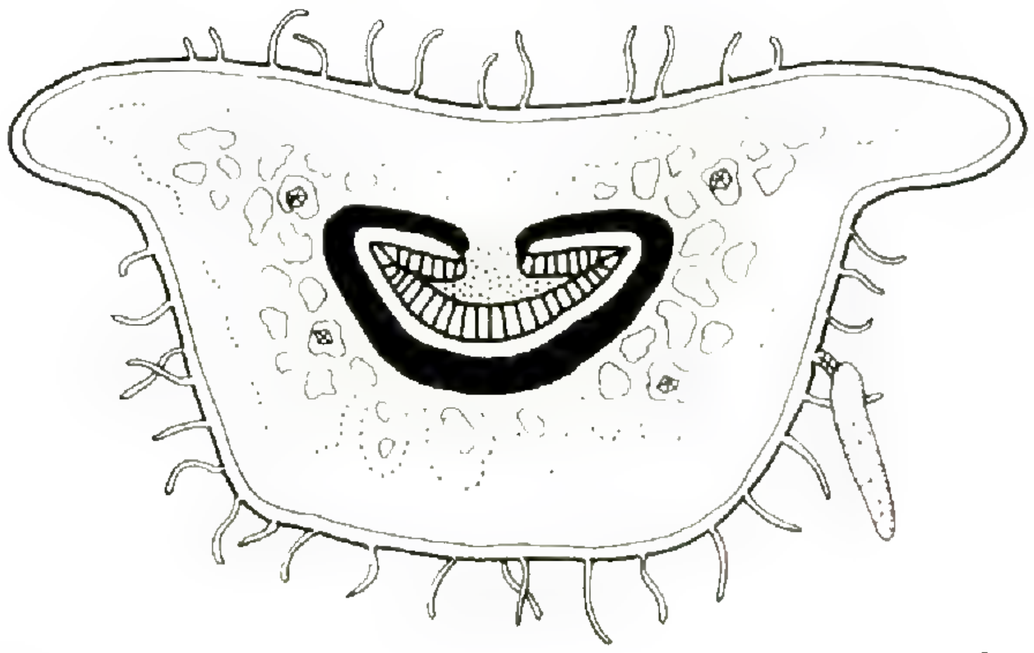

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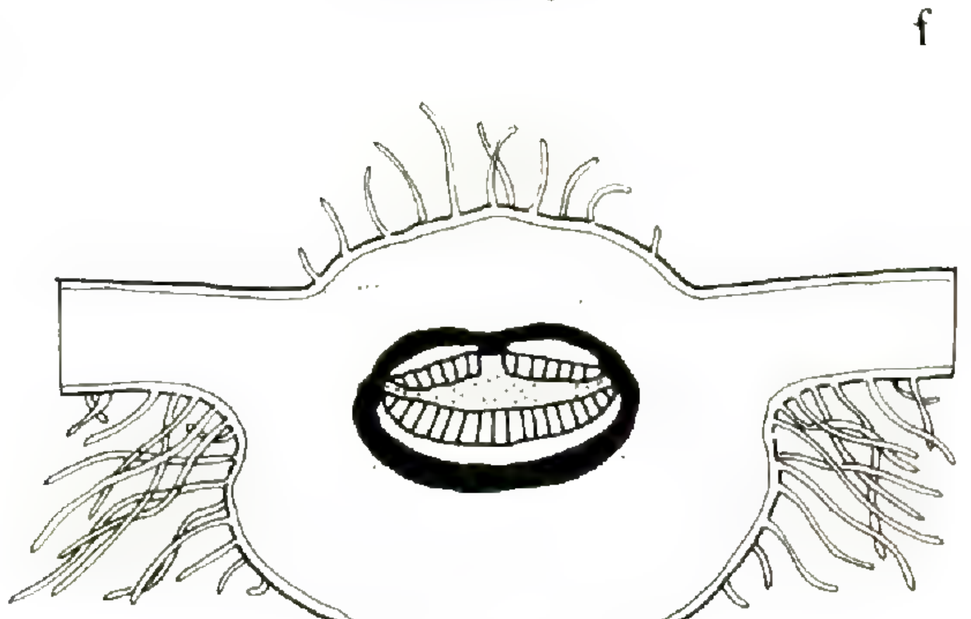

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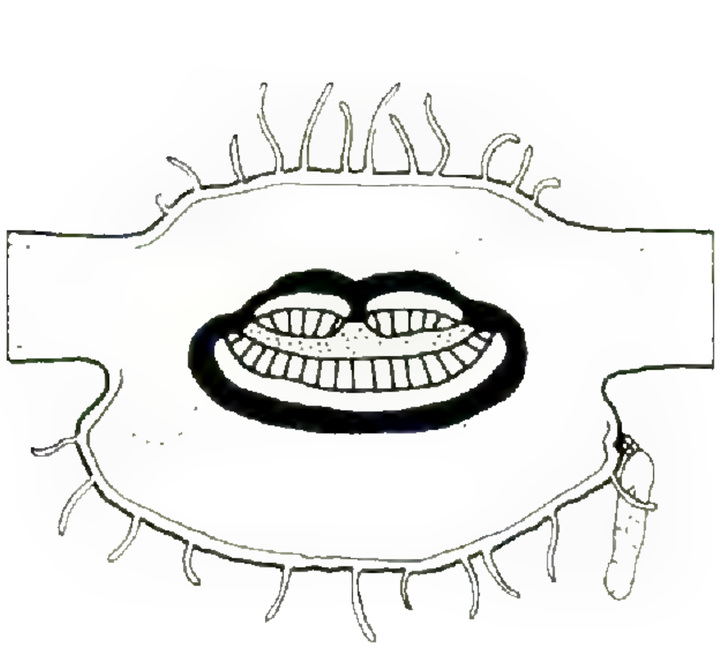

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Cytology

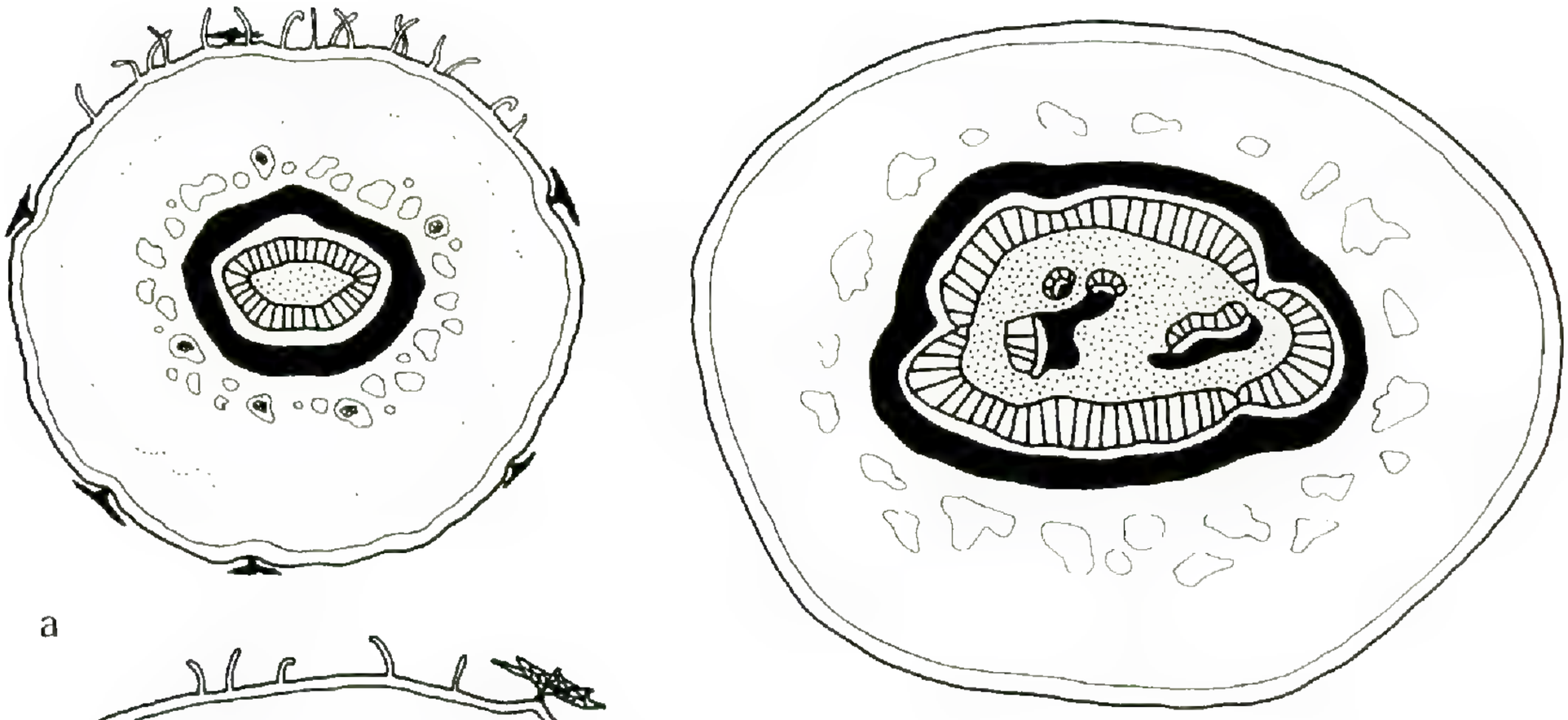
The chromosome numbers of five taxa have been previously recorded. These are *Lyonia mariana*, $2n = 24$ (Callan, 1941); *L. lucida*, $2n = 24$ (Callan, 1941); *L. ovalifolia* var. *foliosa* (reported as *L. foliosa*), $n = 12$ (Larsen, 1966); *L. ovalifolia* (var. *hebecarpa*, since the count was based on Formosan material), $n = 12$ (Chuang *et al.*, 1962); *L. ovalifolia* (var. *ovalifolia*, since the count was based on material from the western Himalayas, India), $n = 12$ (Mehra & Gill, 1968); and *L. ovalifolia* (var. *ovalifolia*, because the count was based on material from Darjeeling, India), $n = 12$ (Mehra & Bawa, 1969).

Meiotic counts have been made of six additional taxa (Table 6). Since all species studied have a diploid number of 24, it is likely that there is little variation in chromosome number; this is especially probable since all four sections are represented in these counts, and since only this number has been reported for the related genera *Pieris* and *Agarista* (see Stevens, 1971). All species investigated have very small chromosomes and show normal meiosis. Raven (1975) suggests that 12, which is widespread within the Ericaceae, may be the family's basic chromosome number, with 13 and 11 being frequent aneuploid derivatives.

VEGETATIVE ANATOMY

Selected features of stem, petiole, and lamina anatomy and leaf venation were studied in all species of *Lyonia* in an effort to discover characters that would be useful in delimiting species and/or higher taxonomic groups. Many of these characters had previously been shown to be quite variable, either within the Ericaceae or within other large angiosperm families (see Gris, 1870; Niedenzu, 1890; Metcalfe & Chalk, 1950; Wood, 1961; Lems, 1964; Watson, 1964, 1965; Stace, 1965; Stevens, 1970, 1971; Howard, 1974). The techniques used were extremely simple. Sections were taken through both nodal and internodal regions of young and older stems, and the leaves were sectioned at intervals up the petiole and into the lamina until the apex was reached. Epidermal peels were prepared for some taxa, and all were studied by the acetone–cellulose acetate method described by Payne (1968). Both dried herbarium specimens and material preserved in FAA were used. The herbarium material was softened by boiling and/or soaking in water, and the sections were cut by hand using a razor blade, and stained using phloroglucinol and hydrochloric acid. The leaves of a few species were embedded in paraffin, sectioned on a microtome, dehydrated, stained with

Figure 14. Cross sections of petioles and leaf midveins of *Lyonia*, × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, and parenchyma cells with stipples). a–c, *L. ovalifolia* var. *lanceolata:* a, extreme base of petiole; b, lower petiole; c, upper petiole. d, *L. ovalifolia* var. *elliptica*, midvein, ca. lower 1/4 of blade. e, *L. ovalifolia* var. *ovalifolia*, upper petiole. f, g, *L. villosa* var. *pubescens:* f, upper petiole; g, midvein, ca. lower 1/4 of blade. h, *L. ligustrina* var. *ligustrina*, upper petiole.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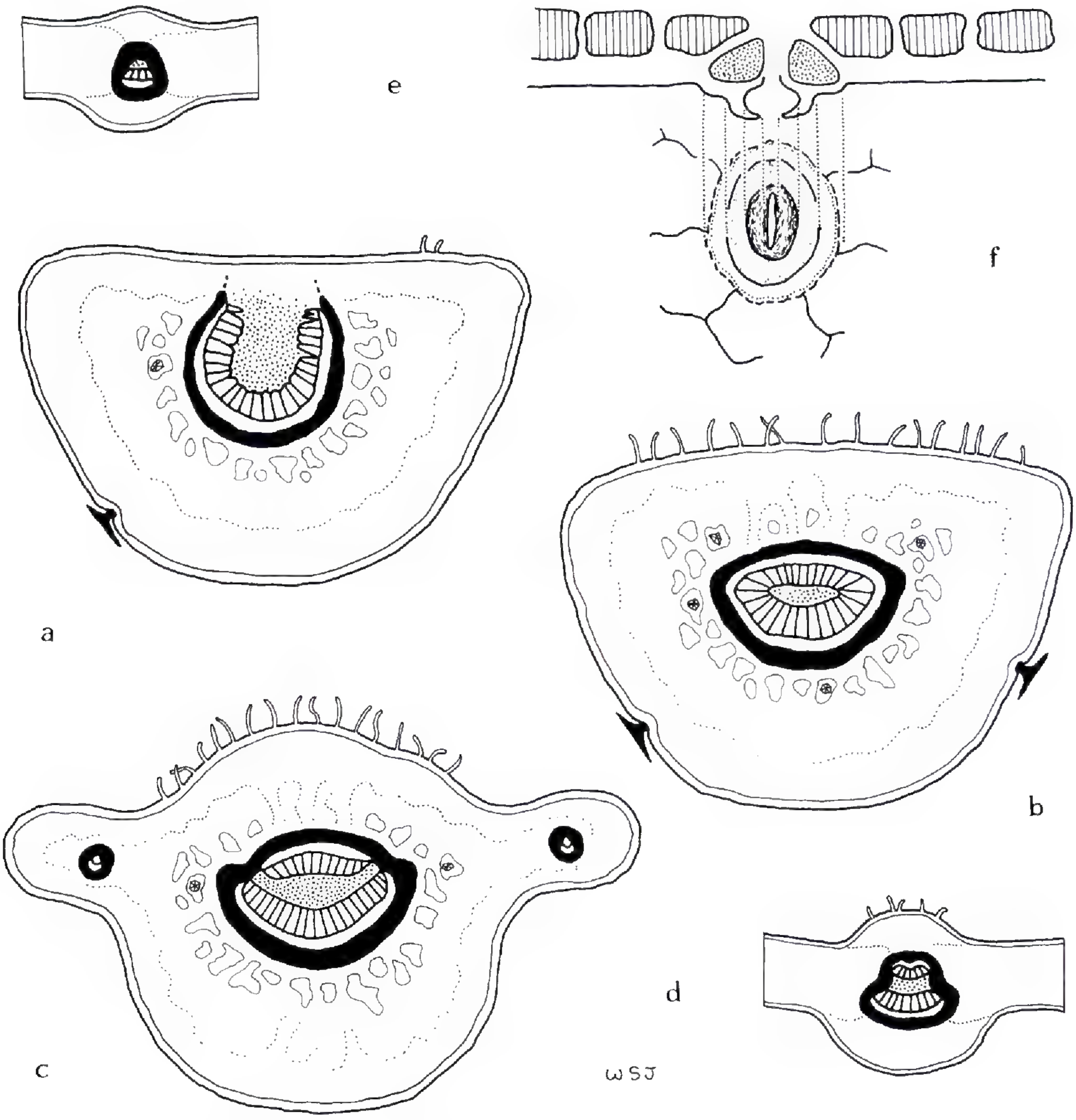

FIGURE 16. a–e, cross sections of petiole and leaf midvein of *Lyonia rubiginosa* var. *costata*, × 25: a, extreme base of petiole; b, lower petiole; c, base of blade; d, midvein, upper 1/4 of blade; e, midvein, near apex. f, diagram illustrating relationship between cross section and surface view of stoma of *L. lucida*.

safranin and fast green, and mounted on slides. Leaves of nearly all taxa were cleared and stained with safranin following the technique of Dilcher (1974). From one to ten leaves (from different specimens) of each species were studied, so in some cases the full range of infraspecific variability

FIGURE 15. Cross sections of petioles of *Lyonia*, × 25 (vascular bundle indicated semidiagrammatically, with fiber sheath in black, phloem in white, xylem with vertical lines, parenchyma cells with stipples). a–c, *L. octandra:* a, lower petiole; b, upper petiole; c, midvein, ca. middle of blade. d, *L. urbaniana*, upper petiole. e–g, *L. buchii:* e, near extreme base of petiole; f, slightly distal to e; g, middle petiole.

may not have been determined. In spite of this possible source of error, several very interesting variations in anatomical characters were discovered within the genus.

STEM ANATOMY AND NODAL TYPE

Cox (1948) studied the xylem anatomy of several species of *Lyonia;* wood anatomy was not investigated in the present study. Two major types of pith are present in the stems of *Lyonia* (see L. Watson, 1965; FIGURE 13 and TABLES 7 and 8): heterogeneous (i.e., cells of two distinct sizes intermingled), with the smaller cells having thickened and lignified walls, in *L. ligustrina;* and homogeneous (i.e., all cells more or less the same size, and lignified) in all other species. All species have characteristic fiber bands in the phloem, the lignified bands developing with increasing age of the twig. There is a sheath of fibers in the pericyclic position in all species, and the phellogen is initiated immediately inside this sheath. Clusters of crystals are frequent in the cortex. All species studied have unilacunar nodes.

LEAF ANATOMY

PETIOLE AND MIDRIB. The single vascular bundle of the petiole is arcuate in shape at the base of the petiole but rapidly becomes deeply arcuate and eventually bifacial (see FIGURES 13, 14, 16) toward the apex. In sect. LYONIA (see TABLE 8 and FIGURES 13, 15, 16) the arms of the arcuate bundle fuse to form a complete cylinder of xylem and phloem within the petiole. In the remaining sections the secondary veins usually begin to depart from the sides of the bundle before this fusion has occurred, and this divides the bundle into an adaxial and an abaxial portion (i.e., it is bifacial). The bundle is always bifacial in all species except *Lyonia lucida,* where it is often unifacial although at least sometimes bifacial near the apex of the petiole (FIGURE 13). In sects. ARSENOCOCCUS and PIERIDOPSIS, and in *L. mariana,* there are often two separate strands of xylem and phloem in the adaxial bundle, but this condition is much less common in sect. LYONIA. In all species the bundle eventually becomes unifacial toward the apex of the leaf. *Lyonia heptamera* and *L. buchii* are unique in that they have medullary bundles within the cylinder of xylem (FIGURE 15). These medullary bundles are derived from the inspiraling and fragmentation of a portion of the adaxial side of the xylem cylinder, which then fuses again into a ring, leaving isolated strands composed of xylem, phloem, and fibers inside the re-formed cylinder. The vascular bundle of all species is surrounded by a ring of fibers. The cortex always contains clusters of crystals, which are usually concentrated in the portion next to the vascular bundle. The petiole is generally more or less round in cross section, with the adaxial surface often slightly flattened and sometimes grooved.

LAMINA. Stomata occur only on the abaxial leaf surface and, in general, are not found on the epidermis over the major (i.e., first-, second-, and third-order) veins. They are anomocytic but appear to be surrounded by one or two rings due to the presence of a cuticular ridge or flange surrounding and forming a chamber over the stomatal opening (FIGURE 16). This chamber may function in reducing water loss in the xeric environments in which many

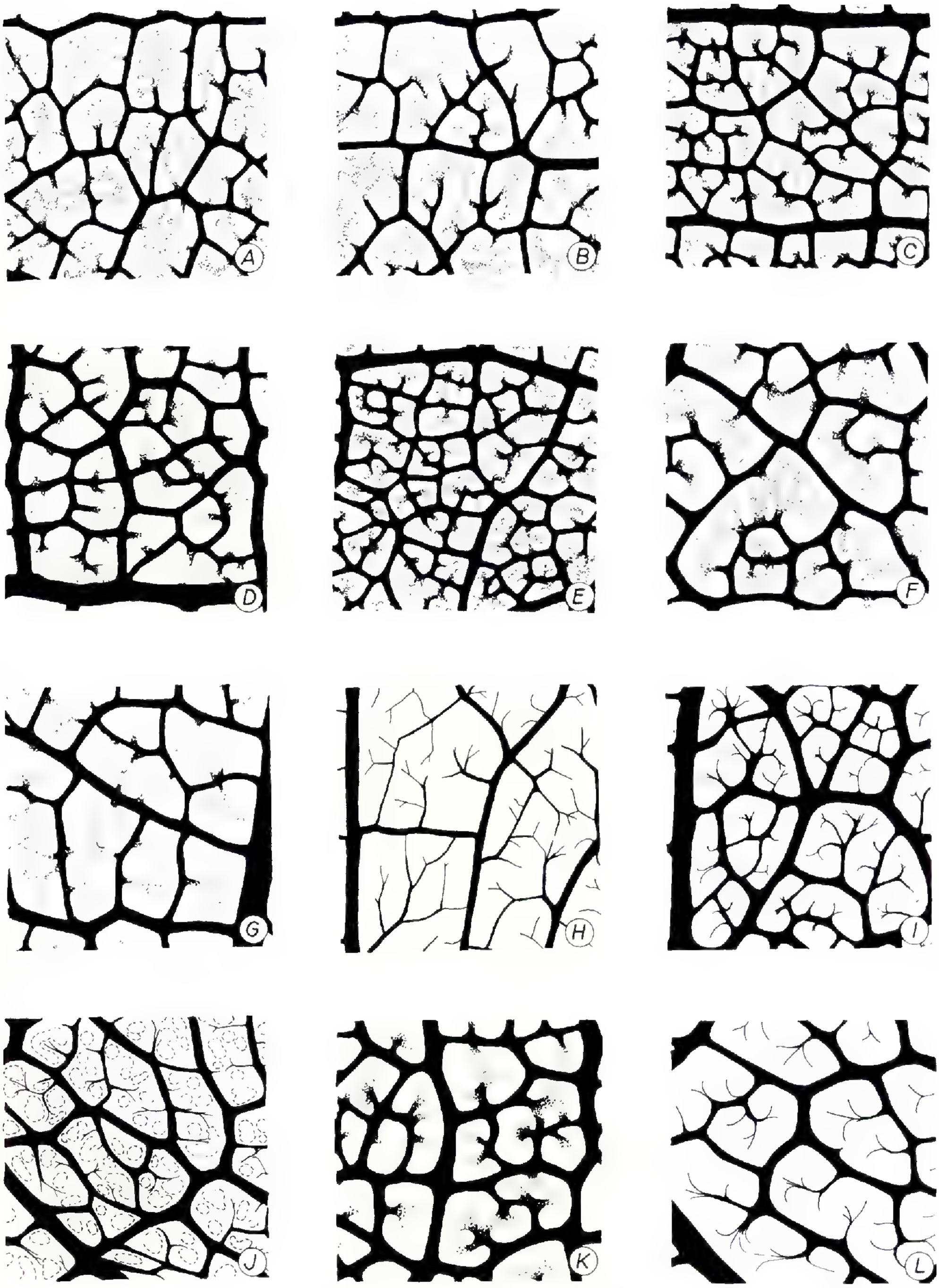

FIGURE 17. Areoles and vein endings of selected species of *Lyonia* (each square = 2.75 sq. mm.): A, *Lyonia ligustrina* var. *foliosiflora;* B, *L. ovalifolia* var. *elliptica;* C, *L. ovalifolia* var. *doyonensis;* D, *L. ovalifolia* var. *lanceolata;* E, *L. macrocalyx;* F, *L. compta;* G, *L. mariana;* H, *L. lucida;* I, *L. truncata* var. *truncata;* J, *L. urbaniana;* K, *L. heptamera;* L, *L. rubiginosa* var. *costata.*

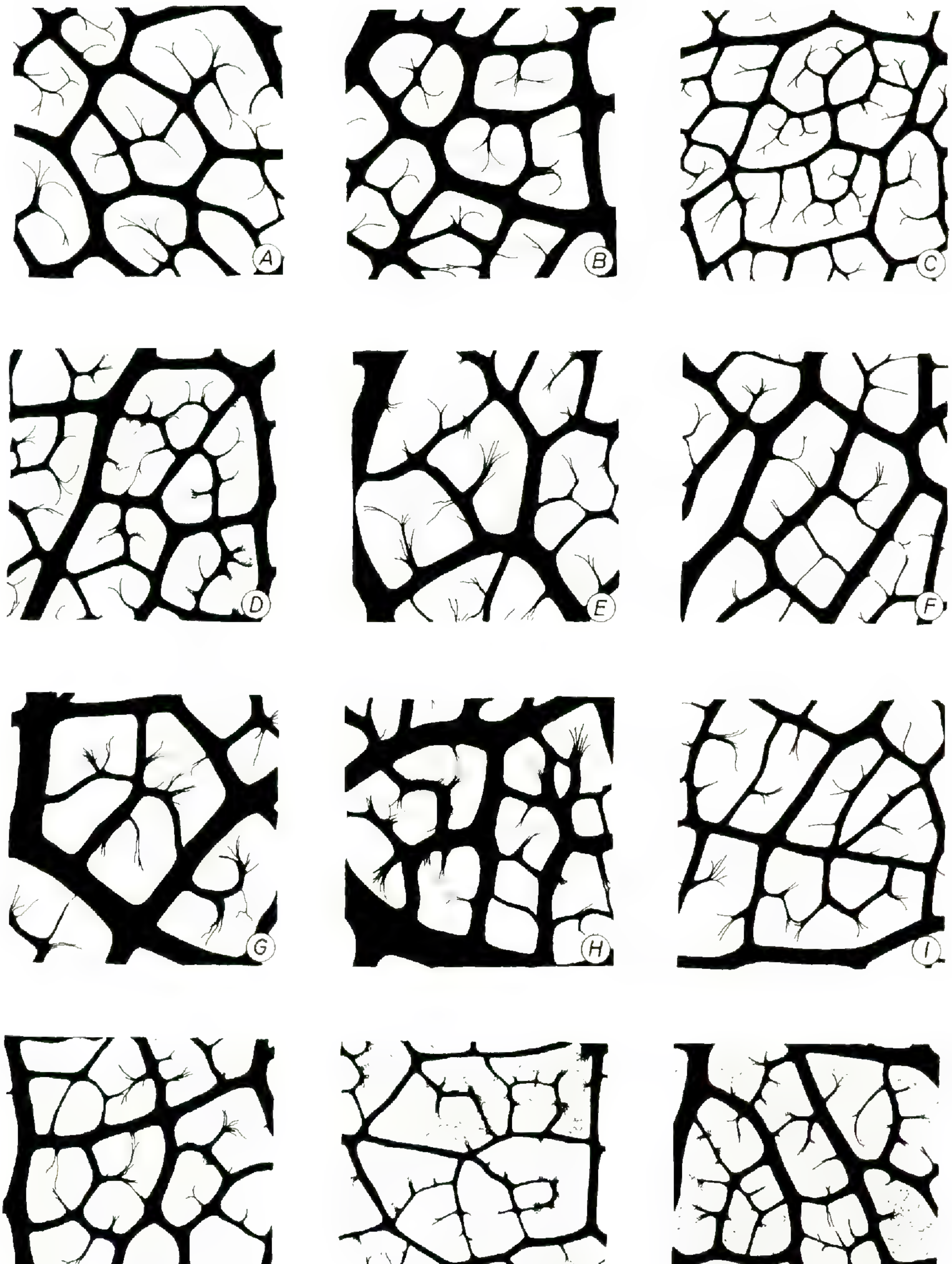

FIGURE 18. Areoles and vein endings of selected species of *Lyonia* (each square = 2.75 sq. mm.): A, *L. alainii;* B, *L. tuerckheimii;* C, *L. jamaicensis;* D, *L. affinis;* E, *L. macrophylla;* F, *L. latifolia* var. *calycosa;* G, *L. nipensis* var. *nipensis;* H, *L. obtusa* var. *obtusa;* I, *L. myrtilloides;* J, *L. glandulosa* var. *revolutifolia;* K, *L. ferruginea;* L, *L. fruticosa.*

species grow. The stomata sometimes show a slight tendency to be oriented with the stomatal aperture parallel to the secondary leaf veins; they also tend to be radially oriented around the bases of the multicellular trichomes, although they are absent immediately adjacent to the bases. Otherwise, orientation is random. The stomata are of several size classes, and small ones, when in the vicinity of a large one, are often arranged with the axes of their apertures pointing toward the larger stoma.

The cuticle is often extremely thick, especially in *Lyonia lucida* and in many species of sect. Lyonia, sometimes reaching slightly over 0.5 mm. In many West Indian taxa it is also often striate, with the striae radially oriented around the peltate scales. The abaxial epidermal cells are usually more or less straight-sided, although they are often somewhat wavy in *L. ligustrina*, *L. lucida*, some varieties of *L. ovalifolia*, and sometimes *L.*

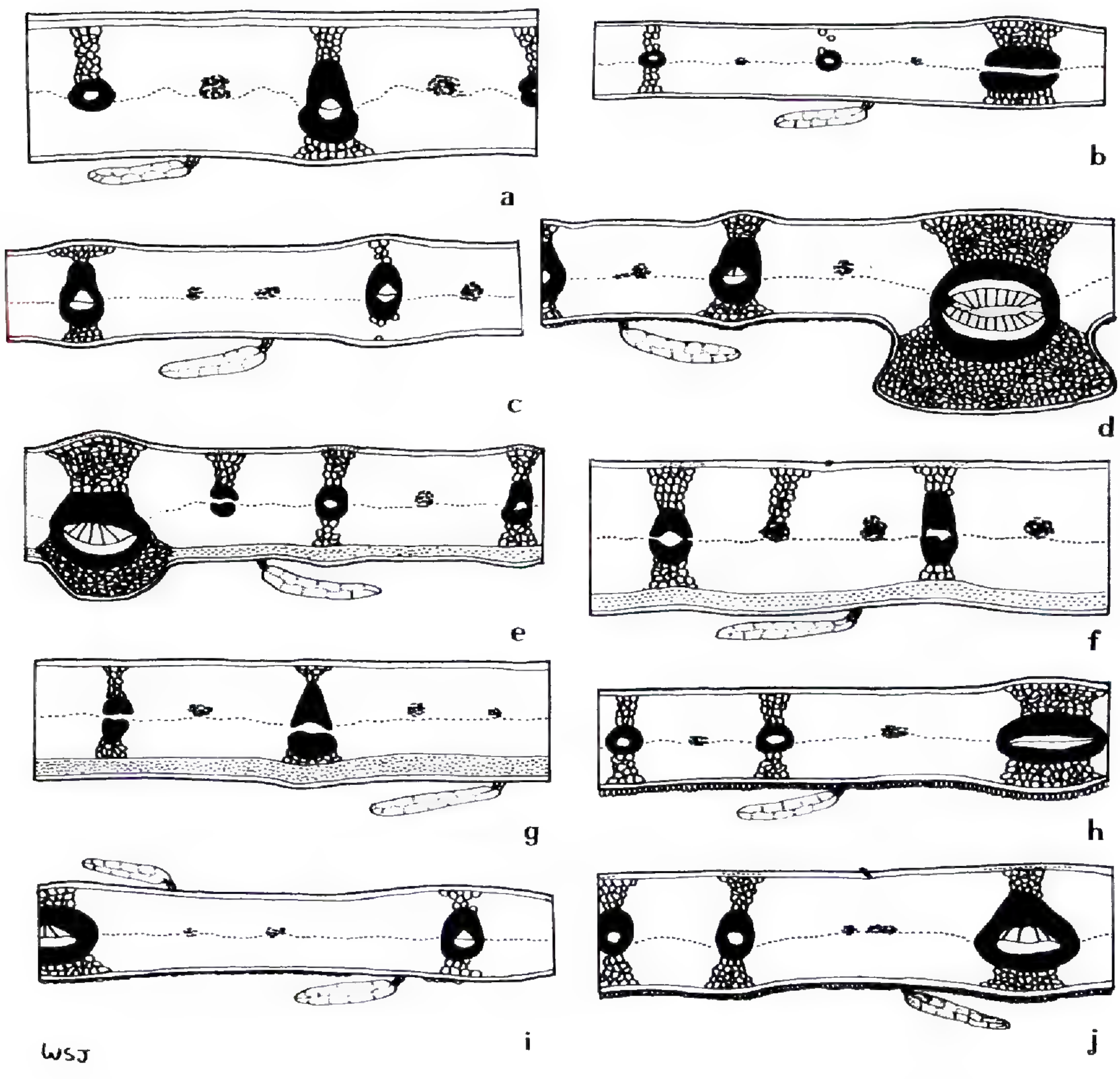

Figure 19. Tranverse sections of leaf blades of various species of *Lyonia* sect. Pieridopsis, × 50 (shaded areas represent lignified cells): a, *Lyonia compta;* b, *L. chapaënsis;* c, *L. ovalifolia* var. *hebecarpa;* d, *L. ovalifolia* var. *doyonensis;* e, *L. ovalifolia* var. *lanceolata;* f, *L. ovalifolia* var. *foliosa;* g, *L. ovalifolia* var. *rubrovenia;* h, *L. macrocalyx;* i, *L. villosa* var. *villosa;* j, *L. villosa* var. *sphaerantha.*

rubiginosa. The adaxial epidermal cells are almost always more or less straight walled. Epidermal cells are usually elongated both over the major veins and in a radial pattern around large, multicellular hairs. When viewed in cross section, they show a wide range of height : breadth ratios (TABLES 7, 8). The epidermal cells are thin walled and unlignified (or are only slightly lignified over the major veins) in the species of sects. PIERIDOPSIS and ARSENOCOCCUS, and in *L. mariana*. The epidermal cells of *L. lucida* are only slightly lignified, but those of the species of sect. LYONIA are usually strongly so. In a related group of Cuban species (TABLE 8), the inner periclinal wall is very prominently thickened and lignified.

Lyonia compta is unusual in that it is the only species among those of sects. PIERIDOPSIS, MARIA, and ARSENOCOCCUS to have a hypodermis (unlignified; see FIGURE 19). Many species of sect. LYONIA (TABLE 8) have a prominent and lignified hypodermis of one or two cell layers (FIGURES 31–33). This character is occasionally of taxonomic importance at the specific level (for example, in distinguishing *L. macrophylla* from *L. ekmanii*, or *L. tuerckheimii* from *L. rubiginosa*). The hypodermis of many species is more strongly developed near the major veins.

Mesophyll tissue is difficult to study from herbarium material, but all species have a well-developed palisade tissue. The number of tiers of cells varies from only one or two (in *Lyonia ligustrina*) to as many as four or five (in *L. lucida*). The walls of the spongy mesophyll cells are usually thin and nonlignified, but in *L. ovalifolia* vars. *lanceolata, foliosa,* and *rubrovenia* one or two layers of spongy tissue next to the abaxial epidermis have thick, lignified walls (FIGURE 19).

The secondary and tertiary veins of many species of sect. LYONIA have no mesophyll tissue either above or below the vascular bundle. In these species the vascular bundle is part of a girder of tissue formed by a group of lignified, thick-walled cells above and below the veins (FIGURES 31–33). This type of "transcurrent" bundle (see Stevens, 1969) contrasts with the vascular bundles of other species (mostly of sects. ARSENOCOCCUS, PIERIDOPSIS, and MARIA; see TABLES 7, 8, and FIGURES 19, 28–30), which are surrounded by chlorophyll-containing mesophyll cells. The bundles of these species are referred to as "embedded." Some species with embedded vascular bundles (e.g., *Lyonia villosa, L. compta, L. macrocalyx,* and some varieties of *L. ovalifolia*) have slightly lignified cells with thin walls and large lumina both above and below the vein, but this condition is quite different from the dense column of lignified, thick-walled, small-lumened cells that occurs in the transcurrent-veined species of sect. LYONIA. *Lyonia buchii* and *L. heptamera* are unusual in that their veins are only semitranscurrent (i.e., the lignified cells surrounding the vascular bundle reach only the adaxial leaf epidermis; FIGURE 31). The pattern of lignified cells surrounding the secondary and tertiary veins is also occasionally useful at the specific or varietal levels; it can be used in distinguishing *L. macrophylla* from *L. obtusa*, or the varieties of *L. nipensis* from each other.

POLLINATION BIOLOGY

From a study of fresh and preserved flowers, it appears that the pollen is shed shortly before the flower opens, but the stigma does not become receptive until soon after this time. The flowers of *Lyonia* are thus slightly protandrous. The stigma is probably receptive when a small viscid droplet is secreted at the tip of the stylar canal.

The flowers of *Lyonia* display a number of characters that are usually associated with pollination by bumblebees (*Bombus*) or other bees (see Knuth, 1909; Faegri & van der Pijl, 1972; Proctor & Yeo, 1973). The flowers are pendulous, very fragrant, and white to slightly pinkish, with cylindrical to urceolate corollas and a hidden, nectar-secreting disc (at the base of the ovary). In all species, the S-shaped and basally swollen filaments serve to hold the anthers in a ring around the style, with the pores directed inward (FIGURE 11). When the filaments are bent outward and are allowed to spring back, the pollen is discharged. The stigma is essentially at the same level as the mouth of the corolla, making the opening, in most species, so small that bees visiting the flower probably cannot fail to come into contact with it. Nectar accumulates at the base of the ovary, where it is held by the pubescence of the ovary and also by the filament bases. Pollination is accomplished when the bee's tongue brushes the curved filaments or small spurs in reaching for the nectar, thus causing pollen to be dusted on its proboscis (Lovell & Lovell, 1935; and pers. obs.). The pollen is then carried to another flower and deposited on the stigma.

Lovell and Lovell (1935) found the flowers of *Lyonia ligustrina* to be almost exclusively pollinated by bumblebees. After observing a large bush for two hours, they noted that all flowers probably received several visits. *Bombus ternarius* was quite abundant, and one individual was seen making 16 visits in one minute. On several occasions the author has seen bumblebees visiting the flowers of this species, and of *L. ferruginea* and *L. fruticosa.* The bees landed on the lower side of a flower cluster, hung onto the flowers, and took nectar from the various flowers of that cluster. The bees then flew to another inflorescence on the same or a nearby shrub (pers. obs). Robertson (1927) has observed bumblebees and other bees (and butterflies) visiting the flowers of *L. ferruginea;* scoliid wasps (*Campsomeris*) have also been seen visiting the flowers of this species (pers. obs.). The author has not seen insects visiting the flowers of any of the West Indian species, but because their floral morphology is similar to that of *L. ferruginea,* they may also be pollinated by various bees.

Lovell and Lovell (1935) covered several panicles of *Lyonia ligustrina* with a fine netting to exclude bees and other large insects. The netted panicles produced many seed capsules, although not as many as the flower clusters that had not been covered. The author has seen occasional fruits developing on isolated greenhouse plants of *L. ferruginea, L. fruticosa,* and *L. lucida,* and it is thus likely that both self- and cross-pollination occur.

ECONOMIC IMPORTANCE

The leaves of *Lyonia mariana* contain the narcotic poison andromedotoxin (a resinoid), a compound also present in several other ericaceous genera. In fact, the species received its common name, stagger-bush, because of the intoxicating effect of its leaves on sheep and cattle (Pammel, 1911; Muenscher, 1939). *Lyonia ligustrina* (Correll & Johnston, 1970; Muenscher, 1939) and *L. ovalifolia* (Sargent, 1893; Wallich, 1820; Brandis & Stewart, 1874) are also said to cause livestock poisoning. Usually the problem is greatest in early spring when the young leaves are emerging.

An infusion of the leaves of *Lyonia ovalifolia* has been employed externally in the treatment of cutaneous diseases, and the young leaves have been said to kill insects (Wallich, 1820; Brandis & Stewart, 1874; Sargent, 1893). Troup (1921) stated that plants of this species are useful in covering hill slopes (in the western Himalayas) and in thus preventing erosion. Many of the West Indian species could also be useful in erosion control and are used for fuel by the local inhabitants. All species of *Lyonia* readily sprout from the base after cutting (or fire) and provide a constant source of firewood if not overused. The leaves of *L. ovalifolia* are rolled for cigarettes by some inhabitants of the Himalayan region.

Several species of *Lyonia* have been used as ornamental shrubs, but none has become very popular. *Lyonia mariana,* with its large, white flowers, is especially beautiful but has a tendency to have a rather straggling habit. *Lyonia lucida, L. macrocalyx, L. ovalifolia, L. villosa, L. ferruginea, L. heptamera, L. rubiginosa, L. buchii, L. urbaniana,* and *L. truncata* also would make beautiful ornamentals, and more study should be directed toward their growth and culture.

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A MONOGRAPH OF LYONIA (ERICACEAE)*

WALTER S. JUDD

TAXONOMIC TREATMENT

Lyonia Nutt. Gen. N. Am. Pl. **1:** 266. 1818, *nomen cons.*, non *Lyonia* Ell. Sketch Bot. S. Carolina Georgia **1:** 316. 1817 (= *Cynanchum* L., Asclepiadaceae), nec *Lyonia* Raf. Med. Repos. New York, ser. 2. **5:** 353. 1803 (= *Polygonella* Michaux, Polygonaceae). *Xolisma* Raf. Am. Mon. Mag. Crit. Rev. **4:** 193. 1819. LECTOTYPE SPECIES: *Lyonia ferruginea* (Walter) Nutt.; see I.C.B.N. 261. 1956, and Rickett & Stafleu, Taxon **9:** 75. 1960.

Neopieris Britton in Britton & Br. Illus. Fl. ed. 2. **2:** 690. 1913. TYPE SPECIES: *Neopieris mariana* (L.) Britton (= *Lyonia mariana* (L.) D. Don).

Desmothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Desmothamnus lucidus* (Lam.) Small (= *Lyonia lucida* (Lam.) K. Koch).

Arsenococcus Small in Small & Carter, Fl. Lancaster Co. 218. 1913. TYPE SPECIES: *Arsenococcus ligustrinus* (L.) Small (= Lyonia *ligustrina* (L.) DC.).

Evergreen or deciduous shrubs or trees, often from an underground, woody, globose to elongated burl, or occasionally forming thickets by means of horizontal underground rhizomes, with terete or angled branches and gray to reddish brown, longitudinally furrowed bark. Indumentum of unicellular hairs and multicellular, biseriate-stalked, ferrugineous, peltate scales or swollen-headed hairs. Buds ovoid to nearly conical or flattened and triangular in outline, usually with 2 outer, imbricate scales, glabrous to densely pubescent. Leaves alternate, estipulate, simple, petiolate, chartaceous to coriaceous, often reddish on young shoots, densely to sparsely covered with peltate scales or swollen-headed hairs on both surfaces, often with unicellular hairs on major veins or densely covering abaxial surface, occasionally papillose or glaucous below; margin entire to irregularly and obscurely toothed, strongly

*Continued from Volume 62, page 128.
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Journal of the Arnold Arboretum **62:** 129–209. April, 1981.

toothed, or serrulate; venation brochidodromous to eucamptodromous with midvein prominent and 3° veins reticulate to percurrent; petiole vascular bundle usually bifacial. Inflorescences axillary, racemose, fasciculate, or paniculate, with each flower perfect, 4- to 7- (or 8-)merous, usually fragrant, in axil of small to large, leaflike bract, with 2 often caducous, lateral bracteoles at or near base of pedicel. Calyx of 4 to 7 (or 8) variously aestivated lobes, usually articulate with pedicel, usually persistent in fruit; corolla cylindrical or urceolate (less commonly campanulate or cylindrical with swollen base), with 4 to 7 (or 8) short, imbricate lobes, white to red, very sparsely to densely covered with peltate scales or swollen-headed hairs (rarely also with few unicellular hairs) on abaxial surface, glabrous on adaxial surface; stamens 8 to 14 (to 16) in 2 whorls, inserted at base of corolla, the filaments flattened, geniculate, roughened, papillose or with long, unicellular hairs, strongly expanded near base, with or without pair of short, spurlike appendages below anther-filament junction, the anthers ± ovoid, papillose, lobes parallel, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, always with white line of disintegration tissue on back of each lobe extending at least along apex of filament and along distal edge of spurs, when present, the pollen tricolporate, surface psilate, indistinctly tectate, in tetrads, without viscin strands; stigma truncate to capitate, obscurely 4- to 7- (or 8-)lobed, minutely papillose, the style columnar, usually at least slightly swollen near base, straight, with 4- to 8-fluted central canal, impressed into apex of ovary and included to slightly exserted, the ovary superior, 4- to 7- (or 8-)locular, glabrous to densely covered with unicellular hairs, peltate scales, or swollen-headed hairs, with placentae axile, positioned subapically to nearly basally on columella, slightly bilobed, bearing numerous anatropous ovules, the nectariferous disc an enlargement of base of ovary wall, variously developed and lobed. Capsules loculicidal, subglobose to ovoid, ellipsoid, or urn shaped, with 4 to 7 (or 8) pale, thickened sutures sometimes separating from valves in dehiscence, the placentae persistent on columella. Seeds very small, brown, oblong-ovoid to linear or spindle shaped, the ends sometimes truncated or with sterile extensions or "tails," the testa loose, thin, composed of single layer of very much elongated, thin-walled cells; embryo small, straight, ± allantoid, white, with 2 small cotyledons, central in cross section, nearer micropylar end, surrounded by fleshy endosperm. Germination epigeal. $2n = 24$.

DISTRIBUTION. Eastern Asia (Japan to Pakistan, south to Malay Peninsula), Greater Antilles (including St. Thomas), and North America (eastern United States and Mexico).

NUMBER OF SPECIES (TAXA). 35 (51).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height, which was recorded in the field or taken from information included on specimen labels, and leaf thickness,

which was measured on thin sections of leaves previously softened in water) included in the descriptions of species have been taken directly from dried herbarium material. The width of the calyx lobes was measured midway between the apex and the point where they join with the adjacent lobes; the width of all other structures was measured at the widest point. All drawings of flowers, stamens, anthers, vegetative rhizomes, and petiole and lamina anatomy were made either from material preserved in FAA or from herbarium material previously expanded and softened by boiling in water with a detergent solution. Drawings of capsules (except for cross sections, which were made from material preserved in FAA), seeds, leaves, and buds were made from dried material.

As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence, distribution, and density of multicellular hairs is described separately. The indumentum of the buds is only mentioned if it differs from that of the stems.

The anatomic variation in the taxa examined has already been treated in the section concerning vegetative anatomy and in TABLE 8.

SPECIMENS EXAMINED

In the citation of herbarium specimens, abbreviations of institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). Specimens are also cited from the private herbarium of Dr. José de Js. Jiménez in Santiago de los Caballeros, Dominican Republic (hereafter referred to as HJ), and from the recently established herbarium of the Jardín Botánico Nacional, "Dr. Rafael M. Moscoso," Santo Domingo, Dominican Republic (hereafter abbreviated as JBM).

In order to conserve space, ordinarily only about 5 to 10 specimens per state have been cited for species in the United States. Similarily, only selected specimens have been cited for species of Mexico, the West Indies, and eastern Asia. Specimens cited are arranged geographically by country and, within the larger countries, by state or province, as follows: United States (Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, Delaware, Maryland, District of Columbia, Virginia, West Virginia, North Carolina, South Carolina, Georgia, Florida, Ohio, Kentucky, Tennessee, Alabama, Mississippi, Missouri, Arkansas, Louisiana, Oklahoma, Texas); Mexico (Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, Puebla, Veracruz, Guerrero, Oaxaca, Chiapas); Cuba (Pinar del Río, Isla de Pinos, Las Villas, Oriente); Haiti; Dominican Republic; Puerto Rico; U. S. Virgin Islands (St. Thomas); Japan (Northern Honshu, Central Honshu, Western Honshu, Shikoku, Kyushu); Taiwan; China (Kiangsu, Anhwei, Chekiang, Kiangsi, Fukien, Kwangtung, Hainan, Honan, Hupeh, Hunan, Kweichow, Kwangsi, Szechwan, Yunnan, Tibet); Vietnam; Laos; Cambodia; Thailand; Malaysia; Burma; Bhutan; Nepal; Bangladesh; India (Arunachal Pradesh, Assam, Nagaland, Manipur, Mizoram, Tripura, Meghalaya, Sikkim, West Bengal, Bihar, Uttar Pradesh, Himachal Pradesh, Punjab, Kashmir); and Pakistan.

1. KEY TO SECTIONS OF LYONIA, INCLUDING SPECIES OF SECTS. ARSENOCOCCUS AND MARIA

1. Abaxial surface of leaves, pedicels, and calyx lepidote. . . . . sect. LYONIA (for species see Key 3).
1. Abaxial surface of leaves, pedicels, and calyx essentially glabrous or pubescent, but not lepidote.
   2. Inflorescences subpaniculate (i.e., racemes of fascicles) or racemose; abaxial leaf surface with scattered, multicellular, extremely long-headed hairs.
      3. Leaves entire; inflorescences racemose. . . . . sect. PIERIDOPSIS (for species see Key 2).
      3. Leaves serrulate; inflorescences subpaniculate. . . . . sect. ARSENOCOCCUS; one species, 6. *L. ligustrina*.
   2. Inflorescences fasciculate; abaxial leaf surface with scattered, multicellular, chiefly short-headed hairs. . . . . sect. MARIA (two species).
      4. Leaves persistent, rigidly coriaceous, with intramarginal vein; corollas usually pink, swollen at base, 2–5 mm. wide; filaments merely roughened; capsules ovoid to ovoid-globose, apex not constricted to only slightly so. . . . . 8. *L. lucida*.
      4. Leaves thinner, deciduous, lacking intramarginal vein; corollas usually white, not swollen at base, 4.5–9 mm. wide; filaments long-pubescent, especially near base; capsules urn shaped, apex usually strongly constricted. . . . . 7. *L. mariana*.

2. KEY TO THE SPECIES OF LYONIA SECT. PIERIDOPSIS*

1. Capsules essentially lacking thickened sutures.
   2. Leaves with the apex acute to obtuse or rounded with short mucro, the secondary veins often slightly sinuous, varying in strength and angle of divergence from midvein, the lamina 1.8–4.1 by 0.5–1.7(–2.2) cm.; floral buds generally above vegetative buds; calyx lobes 1–2(–2.4) by 0.7–1.7 mm. . . . . 1. *Lyonia compta*.
   2. Leaves with the apex long-acuminate to acuminate, often curved, the secondary veins smoothly arching toward margin, the lamina 3.5–9.5 by 1.4–2.7 cm.; floral buds generally below vegetative buds; calyx lobes 2–2.7 by 0.6–0.8 mm. . . . . 2. *L. chapaënsis*.
1. Capsules with slightly to strongly thickened, prominent sutures.
   3. Filaments each with 2 spurs near apex; inflorescences (1.5–)2–16(–30) cm. long. . . . . 3. *L. ovalifolia*.
   3. Filaments lacking spurs; inflorescences 0.5–5.5(–7) cm. long.
      4. Calyx lobes (2–)3–5(–6.5) by 0.5–1.8(–2) mm., never lobed or divided; leaf apex rounded-mucronate, or acute to obtuse with small to elongated mucro, rarely short-acuminate; inflorescence axis glabrous to densely pubescent. . . . . 4. *L. villosa*.
      4. Calyx lobes 4.5–9(–11) by 1.5–5.5(–7) mm., occasionally lobed or divided; leaf apex usually long-acuminate; inflorescence axis glabrous. . . . . 5. *L. macrocalyx*.

*Specimen to be identified must have flowers and capsules (persisting from previous season); otherwise, Key 2a should be used.

2a. Key to the Species of Lyonia Sect. Pieridopsis

1. Inflorescences strongly ascending; flowers pendulous but not secund; floral buds generally above vegetative buds; capsules lacking thickened sutures; leaves persistent *and* with secondary veins ± irregular and scarcely more prominent than tertiary veins. . . . . .1. *Lyonia compta.*
1. Inflorescences usually horizontal to slightly ascending; flowers pendulous and secund; floral buds generally below vegetative buds; capsules with thickened sutures (except in *L. chapaënsis*); leaves deciduous to persistent, the secondary veins irregular or smoothly arching toward margin, usually more prominent than tertiary veins.
2. Calyx lobes elongated, 1.5–5.5(–7) mm. wide at midpoint, occasionally lobed or divided, abaxial surface papillose; leaves semipersistent, 4–13 cm. long, 2–3.5 times longer than wide, with long-acuminate apices *and* with abaxial surfaces papillose and glaucous; filaments without spurs. . . . . .5. *L. macrocalyx.*
2. Calyx lobes small to elongated, 0.7–1.7(–2.5) mm. wide at midpoint, never lobed or divided, abaxial surface papillose or not, but if papillose, then leaves not long-acuminate; leaves extremely variable but without above combination of characters.
3. Secondary veins ± irregular, interconnections often clearly visible.
4. Filaments lacking spurs; corollas urceolate, globose, or cylindrical; inflorescences (0.5–)1–4(–7) cm. long, often appearing ± foliaceous-bracted throughout; leaf apices rounded-mucronate, or acute or obtuse with small to elongated mucro, only rarely short-acuminate. . . . . .4. *L. villosa.*
4. Filaments each with 2 spurs near apex; corollas cylindrical; inflorescences (1.5–)2–13(–20) cm. long, usually with few foliaceous bracts near base; leaf apices long- to short-acuminate. . . . . .3. *L. ovalifolia* (in part).
3. Secondary veins smoothly arching toward leaf margin, interconnections often ± obscure.
5. Leaves with margin not undulate, the lamina acuminate to short-acuminate, mucronate, acute, or obtuse at apex, with acumen usually shorter and less curved than below; filaments 3–9 mm. long; corollas 5–13 mm. long; capsules with sutures strikingly to slightly thickened, glabrous to occasionally densely short-pubescent (hairs to ca. 0.2–0.3 mm. long). . .3. *L. ovalifolia* (in part).
5. Leaves with margin slightly and irregularly undulate, the lamina usually with long, often curved, acuminate apex; filaments ca. 3 mm. long; corollas 4.5–5.5 mm. long; capsules ± lacking thickened sutures, moderately to densely pubescent (hairs to ca. 0.5 mm. long). . . . . 2. *L. chapaënsis.*

3. Key to the Species of Lyonia Sect. Lyonia

1. Lamina with a dense covering of unicellular hairs on abaxial surface, or at least with a few such hairs near apex or margin of some leaves.
2. Leaves with veins prominently and coarsely raised-reticulate (raised ca. 0.2–0.4 mm.) on abaxial surface, petiole and midvein of adaxial surface lacking unicellular hairs, [petiole with medullary bundles within xylem cylinder]; corollas 7–13 mm. wide; capsules 5.5–10.5 mm. wide, 6- or 7-valved.

3. Leaves to ca. 13 cm. long, cuneate to rounded at base, even quaternary and higher order veins slightly depressed on adaxial surface; corollas widely urceolate to campanulate; ± erect shrub to ca. 6 m. trees. . . . . 10. *Lyonia buchii.*
3. Leaves usually not over ca. 6 cm. long, cordate at base (to cuneate in immature plants), quinary and higher order veins ± obscure on adaxial surface; corollas urceolate; widely branched shrub, usually not over ca. 2 m. . . . . 9. *L. heptamera.*

2. Leaves with veins obscure to finely raised-reticulate (raised up to ca. 0.15 mm.) on abaxial surface, petiole and at least extreme proximal portion of midvein of adaxial surface with unicellular hairs, [petiole lacking medullary bundles within xylem cylinder]; corollas 1–6.5 mm. wide; capsules 1–6 mm. wide, mainly 4- and/or 5-valved.
4. Calyx lobes ± densely lepidote on both surfaces, 3.5–6 mm. long; corollas always densely lepidote, scales usually yellowish gold. . . . . 30. *L. latifolia.*
4. Calyx lobes abaxially sparsely to densely lepidote, adaxially at most with few scales near margins, 0.5–3(–4) mm. long; corollas sparsely to densely lepidote, the scales rusty to reddish, brownish, or orangish, but not strikingly yellowish gold.
5. Articulation between pedicel and capsule not developed, pedicel appearing swollen just below capsule; capsules small, very narrowly ovoid, only 1–2 mm. wide, always 4-valved; leaves entire; corollas 2–3 mm. long; calyx lobes 0.5–1 mm. long.
6. Entire leaf slightly to strongly recurved, the veins, or at least the midvein, often depressed, the lamina obovate to elliptic or narrowly elliptic, ca. 1.5–7 times as long as wide, acute to rounded at apex, adaxial surface often roughened (sometimes obviously so only near margin or apex). . . 32. *L. glandulosa.*
6. Leaves flat, the veins not depressed, the lamina orbicular to broadly obovate, less than twice as long as wide, apex always rounded, adaxial surface not roughened. . . . 31. *L. toaënsis.*
5. Articulation between pedicel and capsule ± prominent, or at least visible as slight constriction; capsules narrowly to widely ovoid or ellipsoid to subglobose, 1.5–7 mm. wide, 5- and/or 4-valved; leaves entire or obscurely to irregularly toothed; corollas 3–8 mm. long; calyx lobes 0.9–3(–4) mm. long.
7. Leaves with veins of abaxial surface moderately to strongly, and finely raised-reticulate (secondary through quinary veins raised, although often not visible without magnification), the adaxial surface sometimes rough; capsules ± narrowly ovoid (to sometimes ovoid in *L. urbaniana*), 1.5–3.5 mm. wide.
8. Leaves widely ovate to widely elliptic, not much longer than wide, length/width ratio mostly less than 1.6; scales of new growth orangish to orange-brown; corollas 2–4 mm. long; capsules on individual plant 4- (or 4- and 5-)valved, 1.5–2(–2.5) mm. wide. . . . . 13. *L. microcarpa.*
8. Leaves ovate to elliptic, from much longer to ca. slightly less than twice as long as wide, length/width ratio mostly greater than 1.6; scales of new growth tan to ± dark brown; corollas 3–5.5 mm. long; capsules on individual plant 5- and/or 4-valved, (1.5–)2–3.5 mm. wide.

9. Leaves usually to 3 or 4 cm. long, adaxial surface smooth, abaxial surface usually not densely dark brown lepidote; capsules nearly always 5-valved, elongate-ovoid, usually with slightly constricted apex, the valves slightly S-shaped. . . . . 12. *L. tinensis.*

9. Leaves not over ca. 2.5 cm. long, adaxial surface roughened, abaxial surface often densely brownish lepidote; capsules 5- and/or 4-valved, ± ovoid, the apex not constricted, the valves straight sided or convex. . . . . .11. *L. urbaniana.*

7. Leaves with veins of abaxial surface obscure, or if visible, then only slightly or laxly reticulate (higher order veins not raised), the adaxial surface never rough; capsules ovoid or ellipsoid, to subglobose, (2–)2.5–7 mm. wide.

10. Flowers 4-merous; capsules long-ovoid, 2–3 times as long as wide, 2–3(–3.5) mm. wide. . . . . 23. *L. elliptica.*

10. Flowers mainly 5-merous (but often 4-merous in *L. alpina,* which has leaves 1–3 by 1–2 cm.); capsules ovoid or ellipsoid to subglobose, 1–2 times as long as wide, 2.5–7 mm. wide.

11. Corollas ± densely lepidote, long-urceolate; capsules 4–7 mm. wide; calyx lobes 1.2–3(–4) mm. long; leaves entire. . . . . 24. *L. nipensis.*

11. Corollas only sparsely lepidote, ± cylindrical or long- to short-urceolate; capsules 2.5–5(–6) mm. wide; calyx lobes 1–2.5 mm. long; leaves irregularly to obscurely toothed or notched, or entire.

12. Corollas shortly urceolate, 2–5 by 2–4 mm., usually nearly as wide as long; underground rhizomes often produced.

13. Capsules usually subglobose to shortly ovoid, 2.5–4(–5) mm. long; leaf blades ± flat, the major veins usually not depressed on adaxial surface, the scales of abaxial surface ± persistent, often dark orange; [montane regions; most individuals lacking unicellular hairs on abaxial leaf surface] . . . . . .33. *L. squamulosa* (in part).

13. Capsules ovoid, oblong-ovoid, or ellipsoid, 3–6 mm. long; leaf blades ± flat to strongly recurved, major veins not depressed to strongly so, scales of adaxial surface deciduous to persistent [Coastal Plain].

14. Flowering branches rigidly ascending, flowers frequent on present year's branchlets (although some flowers also borne on branches of previous year), with leaves conspicuously reduced toward branch tips; leaves ± flat, the major veins not depressed, the scales of abaxial surface usually all large and erose, often deciduous; small shrub to 1.5(–3) m. tall. . . . . 35. *L. fruticosa* (in part).

14. Flowering branches more laxly held, flowers nearly always restricted to previous year's branches, leaves not conspicuously reduced toward branch tips; leaves ± flat to strongly recurved, major veins usually depressed, often with scales of 2 sizes (large and ± erose, and smaller, more nearly entire), at least smaller scales ± persistent, or all scales ± large and persistent; shrub or small tree to ca. 6(–10) m. tall. . . . . 34. *L. ferruginea.*

12. Corollas cylindrical or occasionally long-urceolate, 4–8 by 2–5 mm., always clearly longer than wide; underground rhizomes not produced.

15. Leaves with the secondary veins on adaxial surface more prominent than tertiary and higher order veins, usually clearly joining together in series of arches, the abaxial surface with secondary veins ± visible and connected together; [inner periclinal walls of adaxial leaf epidermis strongly lignified and thickened]. . . . . 22. *L. affinis.*

15. Leaves with the secondary veins on adaxial surface not much more prominent than tertiary or higher order veins, so not clearly joined together in series of arches, or all veins ± obscure, the abaxial surface with secondary veins obscure to slightly visible, interconnections nearly always obscure; [inner periclinal walls of adaxial leaf epidermis lignified, but no thicker than other epidermal walls].

16. Leaves with the apex acuminate to acute, or rounded-truncate, the abaxial surface with tertiary and higher order veins visible and slightly reticulate; capsules ellipsoid to widely so, 3.5–6 mm. wide. . . . . 18. *L. rubiginosa* (in part).

16. Leaves with the apex acute to truncate, usually not acuminate, the abaxial surface with tertiary and higher order veins obscure to very slightly reticulate; capsules ovoid or ellipsoid to subglobose, 3–4.5(–5) mm. wide.

17. Capsules subglobose or globose to short-ovoid, 3–4 mm. long and wide, 4- and 5-valved; leaves strongly coriaceous, ca. 0.5–0.6 mm. thick, ± densely lepidote beneath.. . . . . 14. *L. alpina.*

17. Capsules ovoid to ellipsoid, (3–)4–6.5 by 3–4.5(–5) mm., almost exclusively 5-valved; leaves less coriaceous, ca.

0.3–0.4 mm. thick, only sparsely or moderately lepidote beneath. . . . . 15. *L. truncata.*

1. Lamina completely lacking unicellular hairs on abaxial surface (although they may be present on midvein or some secondary veins).
   18. Margin of distal half of leaves definitely and ± irregularly toothed.
      19. Flowers exclusively 4-merous; lamina rounded to widely cuneate or slightly cordate at base, thinly coriaceous, ca. 0.15–0.2 mm. thick, ca. 2–5.5 cm. wide. . . . . 29. *L. maestrensis.*
      19. Flowers 5- (rarely 4-)merous; lamina narrowly to widely cuneate (to rounded) at base, moderately to strongly coriaceous, ca. 0.2–0.45 mm. thick, ca. 1–4 cm. wide (but if flowers 4-merous, then only 1–3 cm. wide).
         20. Corollas shortly urceolate, 3.5–4.5 mm. long, about as wide as long; capsules subglobose to globose or nearly so, moderately to densely pubescent; young stems glabrous to sparsely pubescent. . . . . 16. *L. alainii* (in part).
         20. Corollas ± cylindrical, 4.5–10 mm. long, longer than wide; capsules usually ellipsoid to ovoid, usually only sparsely pubescent; young stems glabrous to densely pubescent.
            21. Young stems thick, 2–3.5 mm. wide near base of flowering or fruiting branches, wider in vigorous young shoots, densely pubescent; capsules 3–5 mm. wide, 5-valved; leaves coriaceous, ca. 0.35–0.45 mm. thick. . . . . 17. *L. tuerckheimii.*
            21. Young stems thinner, 1.2–2.3 mm. wide near base of flowering or fruiting branches, wider in vigorous young shoots, usually nearly glabrous or only sparsely pubescent; capsules 1.7–3.5(–4.5) mm. wide, 5- and/or 4-valved; leaves thinner, ca. 0.2–0.35 mm. thick. . . . . 18. *L. rubiginosa* (in part).
   18. Margin of distal half of leaves entire to undulate or very obscurely toothed.
      22. Capsules narrowly ovoid, 1.7–3(–3.5) mm. wide, mainly 4-valved (although rare individuals with mainly 5-valved capsules occur in *L. myrtilloides*); corollas 2.5–4.5 mm. long; petioles 1.5–6 mm. long.
         23. Leaves often uniformly small on strongly ascending branches, often obovate, to elliptic or widely elliptic, secondary veins ± irregular and often very obscure on abaxial surface, apex rounded to truncate; pedicels 2.5–11 mm. long. . . . . 28. *L. myrtilloides.*
         23. Leaves not uniformly small on strongly ascending branches, ± elliptic to ovate, secondary veins ± regular and ± apparent on abaxial surface, apex acuminate or acute to rounded or truncate; pedicels 1.5–4.5 mm. long.
            24. Capsules long-ovoid, 2.5–5 mm. long, length/width ratio of valves 3–4; young twigs sparsely to densely pubescent; corollas 3–4.5 mm. long. . . . . 21. *L. trinidadensis.*
            24. Capsules very shortly ovoid, 2.5–4.3 mm. long, length/width ratio of valves 2–3.3; young twigs essentially glabrous; corollas 2.5–4 mm. long. . . . . 20. *L. octandra.*

22. Capsules ellipsoid or ovoid, to subglobose, (2.5–)3–6 mm. wide, mainly 5-valved (usually 4-valved in *L. ekmanii*, which has ovoid capsules 4–4.5 mm. wide); corollas 2.5–7 mm. long; petioles 1.5–15 mm. long.
    25. Corollas shortly urceolate, 2.5–5 by 2.5–4 mm., as wide as long or nearly so; capsules subglobose to globose or ovoid, 2.5–5 mm. long and wide.
        26. Leaves coriaceous, ca. 0.34–0.44 mm. thick, not flexible or only slightly so when dried, not markedly reduced in size toward ends of branches, the margin usually obscurely toothed or notched (or clearly toothed), the apex acute to rounded or truncate but never acuminate, the scales of abaxial surface ± widely spaced, with margins entire to undulate; neither elongated woody burl nor rhizomes present. . . . . 16. *L. alainii* (in part).
        26. Leaves thinner, ca. 0.17–0.27 mm. thick, more flexible, sometimes markedly reduced in size toward ends of branches, the margin usually entire or undulate, occasionally obscurely toothed, the apex acuminate or acute to rounded, the scales of abaxial surface widely spaced to overlapping, with margins ± undulate to erose; elongated woody burl and often rhizomes present.
            27. Capsules usually subglobose to shortly ovoid; leaves only sometimes quite strongly reduced in size toward flowering branch tips, the abaxial surface with ± persistent peltate scales; [montane taxon]. . . . . 33. *L. squamulosa* (in part).
            27. Capsules ovoid to ellipsoid; leaves always ± conspicuously reduced in size toward ends of rigidly ascending flowering branches, the abaxial surface with ± deciduous scales; [Coastal Plain taxon; most individuals have a dense covering of unicellular hairs on abaxial leaf surface]. . . . . 35. *L. fruticosa* (in part).
    25. Corollas cylindrical to long-urceolate, 4–7 by 2–4.5 mm., always longer than wide; capsules ovoid to ellipsoid, 3.5–9 by 2.5–6 mm.
        28. Calyx lobes 1.3–2.5(–3) mm. long; corollas long-urceolate; capsules 3.5–9 by 3.5–6 mm.; leaves rounded or truncate to acute or nearly so at apex, at least proximal portion of abaxial midvein sometimes with unicellular hairs; filaments usually with 2 minute spurs near junction with anthers.
            29. Capsules ± ovoid with straight-sided valves; pedicels 8–30 mm. long; leaves with abaxial surface sparsely lepidote, with ca. 10 to 40 ± entire-margined scales/5 sq. mm., the petiole 1.5–5(–9) mm. long. . . . . 25. *L. obtusa*.
            29. Capsules ± ellipsoid to ovoid with usually convex valves; pedicels 4–12 mm. long; leaves with abaxial surface moderately lepidote, with ca. 60 to 140 more irregularly margined scales/5 sq. mm., the petiole 4–15(–18) mm. long.

30. Twigs densely pubescent; flowers 5-merous; capsules 4.5–8.5 mm. long.. .26. *L. macrophylla.*
30. Twigs essentially glabrous; flowers mainly 4-merous; capsules 3.5–5 mm. long. . . . . 27. *L. ekmanii.*

28. Calyx lobes 0.6–2 mm. long; corollas usually ± cylindrical; capsules 3.5–6 by 2–4 mm.; leaves acute or acuminate to rounded or truncate at apex, abaxial midvein lacking unicellular hairs; filaments lacking spurs.
    31. Young twigs usually only sparsely pubescent; leaves with length/width ratio of 1.5–2.5(–3.5), margin obscurely and irregularly toothed to ± entire, secondary veins sometimes slightly depressed; corollas 4–6 mm. long; [cloud forests]. . . 18. *L. rubiginosa* (in part).
    31. Young twigs usually moderately pubescent; leaves with length/width ratio of 2–4, margin entire or nearly so, secondary veins almost never depressed; corollas (4–)4.5–7 mm. long; [mainly dry slope forest and thickets]. . . . . 19. *L. jamaicensis.*

The following supplementary keys to the species and varieties of *Lyonia* in Cuba, Hispaniola, Jamaica, and continental North America are included as an aid to those interested in the floras of these areas.

4. Key to the Species of Lyonia in Jamaica

1. Flowers 4-merous, corolla 2.5–4 mm. long; capsules 2.5–4.3 by 2–3 mm.; pedicels up to 4 mm. long; young twigs essentially glabrous; [cloud forests and elfin woodlands, ca. (1230–)1450–2250 m. alt.]. . . .20. *L. octandra.*
1. Flowers 5-merous, corolla (4–)4.5–7 mm. long; capsules 4–6(–7) by 3–4 mm.; pedicels up to 11 mm. long; young twigs sparsely to densely pubescent; [mainly dry slope forests, ca. 150–1300 m. alt.]. . . . 19. *L. jamaicensis.*

5. Key to the Species and Varieties of Lyonia in Hispaniola

1. Leaves with a dense covering of unicellular hairs on abaxial surface or some leaves at least with few such hairs near apex or margin.
    2. Leaves with coarsely raised-reticulate veins on abaxial surface, petiole and midvein of adaxial surface glabrous; corollas carnose, 7–13 mm. wide; calyx lobes (2–)2.5–6 mm. long; capsules 5.5–10.5 mm. wide, 6- or 7-valved.
        3. Leaves to ca. 13 cm. long, cuneate to rounded at base, even quaternary and higher order veins slightly depressed and clearly evident on adaxial surface; corollas widely urceolate to campanulate; ± erect shrub to medium-sized tree to ca. 6 m. tall; [thickets, cloud forests, and pine forests; 800–2100 m. alt.]. . . . . 10. *L. buchii.*
        3. Leaves usually not over ca. 5 cm. long, cordate at base (to cuneate in immature plants), quinary and higher order veins ± obscure on adaxial surface; corollas urceolate; widely branched shrub usually under ca. 2 m. tall; [pine forests, 2000–3175 m. alt.]. . . . . 9. *L. heptamera.*
    2. Leaves with veins obscure to finely raised-reticulate on abaxial surface, petiole and at least extreme proximal portion of midvein of adaxial surface pubescent; corollas not carnose, 1.8–4.5 mm. wide; calyx lobes

0.8–2 mm. long; capsules 1.5–5 mm. wide, 4- or 5-valved.

4. Capsules ovoid or ellipsoid to subglobose, 3–4.5(–5) mm. wide; corollas 4–7 mm. long; leaves with abaxial surface ± obscurely veined, to rarely very slightly and laxly reticulate, adaxial surface ± smooth, lacunae usually not present in cross section (use lens!).
   5. Capsules globose to subglobose or shortly ovoid, 3–4 by 3–4 mm., 4- and 5-valved; leaves strongly coriaceous, ca. 0.5–0.6 mm. thick, abaxial surface ± densely lepidote; [Massif de la Selle, above ca. 2500 m.] . . . . . 14. *L. alpina.*
5. Capsules ovoid to ellipsoid, (3–)4–6.5 by 3–4.5(–5) mm., almost exclusively 5-valved; leaves thinner, ca. 0.3–0.4 mm. thick, abaxial surface sparsely to moderately lepidote.
   6. Leaves 0.8–3.5(–4) cm. long, erect and concave to spreading and ± flat, sometimes slightly recurved; shrub to 2.5(–3) m. tall, often densely branched; [Sierra de Baoruco and Massif de la Selle, ca. 400–1700 m. alt.] . . . . . 15a. *L. truncata* var. *truncata.*
   6. Leaves (2.5–)3–5(–6.8) cm. long, more spreading and usually ± flat to recurved; shrub to small tree often to 3–7 m. tall, branching more open and lax; [Cordillera Central and Massif du Nord, ca. 100–1250 m. alt.] . . . . . 15b. *L. truncata* var. *montecristina.*

4. Capsules ± narrowly ovoid (to ovoid in *L. urbaniana*), 1.5–3.5 mm. wide; corollas 3–5.5 mm. long; leaves with abaxial surface usually moderately to strongly and finely raised-reticulate, adaxial surface sometimes rough, lacunae usually present in cross section.
   7. Leaves broadly ovate to broadly elliptic, length/width ratio mostly less than 1.6; scales of new growth orangish to orange-brown; corollas 3–4 mm. long; capsules on single plant 4- (or 4- and 5-)valved, 1.5–2(–2.5) mm. wide; [Massif de la Selle and Sierra de Baoruco] . . . . . 13. *L. microcarpa.*
   7. Leaves ovate to elliptic, length/width ratio mostly greater than 1.6; scales of new growth usually tan, brown, or dark brown; corollas 3–5.5 mm. long; capsules on single plant 5- and/or 4-valved, (1.5–)2–3.5 mm. wide.
      8. Leaves usually to 3–4 cm. long, the adaxial surface ± smooth, the abaxial surface usually sparsely to moderately lepidote, scales tan to light brown; capsules nearly always 5-valved, elongate-ovoid, apex usually slightly constricted, valves slightly S-shaped; [pine forests of Cordillera Central, ca. 1100–1700 m. alt.] . . . . . 12. *L. tinensis.*
      8. Leaves not over ca. 2.5 cm. long, the adaxial surface rough, the abaxial surface often densely lepidote, scales dark brown; capsules 5- and/or 4-valved, ± ovoid, apex not constricted, valves straight sided or convex; [pine forests of Cordillera Central, ca. 2000–2400 m. alt.] . . . . . 13. *L. urbaniana.*

1. Leaves completely lacking unicellular hairs on abaxial surface (although sometimes pubescent on proximal portion of midvein).
   9. Corollas 3.5–4.5 mm. long, urceolate, about as wide as long; capsules subglobose to globose or nearly so; young stems glabrous or only sparsely pubescent; margins of leaves obscurely to irregularly toothed. . . . . 16. *L. alainii.*

9. Corollas 5.5–10 mm. long, cylindrical, longer than wide; capsules usually ellipsoid or ovoid; young stems nearly glabrous to densely pubescent; margins of leaves more conspicuously toothed.
   10. Young stems thick, 2–3.5 mm. wide near base of flowering or fruiting branches (wider in vigorous young shoots), usually densely pubescent; capsules 3–5 mm. wide, 5-valved; leaves coriaceous, 0.35–0.45 mm. thick; [pine forests and thickets, (1700–)2000–3175 m. alt.]. . . . . .17. *L. tuerckheimii.*
   10. Young stems thinner, 1.2–2.3 mm. wide near base of flowering or fruiting branches (wider in vigorous young shoots), at most sparsely pubescent; capsules 1.7–3.5 mm. wide, 5- and/or 4-valved; leaves thinner, 0.2–0.25 mm. thick; [cloud forests, thickets, and pine forests; ca. 900–2100 m. alt.]. . . . . 18a. *L. rubiginosa* var. *costata.*

6. Key to the Species and Varieties of Lyonia in Cuba

1. Leaves with intramarginal vein, the abaxial surface with stalked, glandular-headed hairs. . . . . .8. *L. lucida.*
1. Leaves lacking clearly defined intramarginal vein, the abaxial surface lepidote, with scales ± ferrugineous, peltate.
   2. Leaves with abaxial surface densely covered with unicellular hairs or at least with a few such hairs near apex or margin.
      3. Articulation between pedicel and capsule absent; corollas 2–3 mm. long; calyx lobes 0.5–1 mm. long; capsules very narrowly ovoid, 1–2 mm. wide, always 4-valved.
         4. Leaves flat, the veins not depressed, the lamina orbicular to broadly obovate, length/width ratio 0.9–1.8, apex always rounded; [rare; mountains near Toa]. . . . . 31. *L. toaënsis.*
         4. Leaves slightly to strongly recurved, at least the midvein depressed, the lamina obovate to elliptic or narrowly elliptic, length/width ratio 1.5–7, apex acute to rounded.
            5. Leaves obovate (to elliptic), 0.5–2 cm. wide, 1.5–3(–3.5) times as long as wide, the distal margin plane, sometimes slightly revolute; [Sierra de Nipe]. . . . . 32a. *L. glandulosa* var. *glandulosa.*
            5. Leaves elliptic to narrowly so, usually not over ca. 1 cm. wide, 2.5–7(–10) times as long as wide, distal margin slightly to strongly revolute; [predominantly in Sierra de Micara, Sierra de Cristal, Sierra de Moa, and near Moa]. . . . . .32b. *L. glandulosa* var. *revolutifolia.*
      3. Articulation between pedicel and capsule present; corollas 3.5–8.5 mm. long; calyx lobes 1–6 mm. long; capsules ovoid to widely so, or ellipsoid, always greater than 2 mm. wide, 5- and/or 4-valved.
         6. Calyx lobes densely lepidote on both surfaces, 3.5–6 mm. long; corollas always densely lepidote; scales yellowish gold; [chiefly in Sierra Maestra, ca. 650–2000 m. alt.].
            7. Leaves with secondary veins at least slightly depressed, the lamina ovate to elliptic or nearly orbicular, length/width ratio 1–1.9, base rounded, slightly cordate, or widely cuneate, the petiole 4–12 mm. long; [Sierra Maestra from Loma del Gato westward]. . . . . .30a. *L. latifolia* var. *latifolia.*
            7. Leaves with secondary veins not depressed, the lamina elliptic

to obovate or ovate, length/width ratio (1.2–)1.4–2.4(–2.7), base narrowly to widely cuneate or less commonly rounded, sometimes decurrent, the petiole 8–20 mm. long; [Sierra Maestra from Loma del Gato east to Gran Piedra range and mountains of eastern Oriente] . . . . . 30b. *L. latifolia* var. *calycosa.*

6. Calyx lobes sparsely to densely lepidote on abaxial surface, at most sparsely lepidote near margins on adaxial surface, lobes 1–3(–4) mm. long; corollas sparsely to densely lepidote; scales rusty to reddish or brownish.
8. Capsules 2–4.5 mm. wide, ovoid to ellipsoid, the valves 4 or 5, convex to straight; corollas sparsely lepidote, ± cylindrical; scales of pedicel and calyx lobes pale orange; leaf base usually cuneate to decurrent (to widely cuneate or rounded when flowers 4-merous).
9. Flowers 4-merous, corolla 2.5–3 mm. wide; capsules long-ovoid, 2–3(–3.5) mm. wide, at least twice as long as wide; [rare and poorly known] . . . . . 23. *L. elliptica.*
9. Flowers 5-merous, corolla (2.5–)3–5 mm. wide; capsules ovoid to ± ellipsoid, 3–4.5 mm. wide, from slightly longer than wide to twice as long as wide; [locally common in Sierra Maestra, ca. 400–700 m. alt.] . . . . . 22. *L. affinis.*
8. Capsules 4–7 mm. wide, ovoid, the valves 5, straight; corollas densely lepidote, usually ± long-urceolate; scales of pedicel and calyx lobes orange to deeply orange-red or brownish; leaf base rounded to widely cuneate or slightly cordate.
10. Leaves with blade ± flat, midvein not depressed to slightly so, secondary veins not depressed, scales of abaxial surface usually irregular margined and deciduous, petiole (2.5–)3–7.5 mm. long; [northern Oriente from Sierra de Nipe to plateau near Moa] . . . . . 24a. *L. nipensis* var. *nipensis.*
10. Leaves with blade usually strongly recurved, the midvein and secondary veins depressed, often strongly so, the scales of abaxial surface of 2 distinct types (some irregular margined and deciduous, smaller ones ± entire and persistent), the petiole 1.5–4 mm. long; [Sierra de Moa and Sierra de Toa only] . . .24b. *L. nipensis* var. *depressinerva.*

2. Leaves with abaxial surface completely lacking unicellular hairs (although such hairs may be present on midvein or some secondary veins).
11. Leaves with margin irregularly toothed, often nearly to base; capsules 4-valved; [little known; Sierra Maestra] . . . . . 29. *L. maestrensis.*
11. Leaves with margin entire to undulate or obscurely toothed (if toothed, teeth only extending from near apex to ca. midpoint of leaf, never present along margin of proximal half); capsules 4- and/or 5-valved.
12. Capsules 3.5–6.5 mm. wide, ellipsoid to ovoid or widely ovoid, 5-valved (but usually 4-valved in *L. ekmanii*); calyx lobes 1.3–2.5(–3) mm. long; corollas 4–7 mm. long; petioles 2–15 mm. long.
13. Capsules ovoid, valves straight; pedicels 8–30 mm. long; leaves with abaxial surface sparsely lepidote, scales ca.

10 to 40/5 sq. mm. and ± entire; petioles 1.5–5(–9) mm. long.

14. Leaf blades to ca. 7 cm. long, usually slightly to strongly recurved, often with midvein and/or secondary veins depressed, abaxial surface with tertiary veins much less prominent than secondary veins and obscure to slightly reticulate, apex predominantly rounded; [Moa-Baracoa region] . . . . . 25a. *L. obtusa* var. *obtusa*.

14. Leaf blades to ca. 3.5 cm. long, ± flat, veins not depressed, abaxial surface with tertiary veins nearly as prominent as secondary veins and strongly reticulate, apex acute to rounded; [Sierra de Cristal] . . . . . 25b. *L. obtusa* var. *longipes*.

13. Capsules ± ellipsoid to ovoid, valves ± convex; pedicels 4–12 mm. long; leaves with abaxial surface moderately lepidote, scales ca. 60 to 140/5 sq. mm. and more irregular margined, petiole 4–15(–18) mm. long.

15. Twigs densely pubescent; flowers 5-merous; capsules 4.5–8.5 mm. long; [common; mountains of northern Oriente from Sierra de Nipe to Moa-Baracoa region] . . . . . 26. *L. macrophylla*.

15. Twigs essentially glabrous; flowers mainly 4-merous; capsules 3.5–5 mm. long; [rare; Pinar del Río] . . . . . 27. *L. ekmanii*.

12. Capsules 1.7–3(–3.5) mm. wide, narrowly ovoid, mainly 4-valved (very rarely 5-valved in *L. myrtilloides*); calyx lobes 0.7–1.5 mm. long; corollas 2.5–4.5 mm. long; petioles 1.5–5.5 mm. long.

16. Leaves obovate, sometimes elliptic or widely so, often uniformly small on strongly ascending branches, the secondary veins ± irregular, often very obscure on abaxial surface, the apex rounded to truncate; pedicels 2.5–11 mm. long; filaments with minute spurs; [pinelands and savannas, Pinar del Río and Isle of Pines] . . . . 28. *L. myrtilloides*.

16. Leaves ± elliptic to ovate, not uniformly small on strongly ascending branches, the secondary veins ± regular, usually evident, the apex acuminate to acute, truncate, or rounded; pedicels 2.5–4.5 mm. long; filaments lacking spurs; [cloud forests and savannas, Sierra de Trinidad and Sierra de Sancti Spiritus of Las Villas Prov.] . . . . . 21. *L. trinidadensis*.

7. Key to the Species and Varieties of Lyonia in Continental North America

1. Abaxial surface of leaves, pedicels, and calyx lepidote.

2. Leaves with abaxial surface usually glabrous but ± persistently lepidote, lamina ± flat, major veins usually not depressed on adaxial surface; capsules usually subglobose to shortly ovoid, 2.5–4(–5) mm. long; [Mexico, Sierra Madre Oriental and mountains of Chiapas] . . . . . 33. *L. squamulosa*.

2. Leaves with abaxial surface usually sparsely to densely pubescent and deciduously or persistently lepidote, lamina flat to strongly recurved, major veins not depressed to strongly so; capsules ovoid, oblong-ovoid,

or ellipsoid, 3–6 mm. long; [Coastal Plain, southeastern United States].

3. Ultimate branchlets rigidly ascending, flowers frequent on present year's branchlets (although some flowers also borne on branches of previous year), with leaves conspicuously reduced toward branch tips; leaves with the distal margin at most slightly revolute, the major veins not depressed, the abaxial surface with scales usually all large and ± irregular margined, often deciduous; small shrub to 1.5(–3) m. tall. . . . . .35. *L. fruticosa.*

3. Ultimate branches not rigidly ascending, flowers nearly always restricted to previous year's branches, with leaves not conspicuously reduced toward branch tips; leaves with the distal margin usually revolute, sometimes strongly so, the major veins usually depressed, the abaxial surface with some scales often large and irregular margined, others smaller and more nearly entire, at least smaller scales ± persistent (or all scales ± large and persistent); shrub or small tree to ca. 6(–10) m. tall. . . . . 34. *L. ferruginea.*

1. Abaxial surface of leaves, pedicels, and calyx nearly glabrous or pubescent, but not lepidote.

4. Inflorescences subpaniculate; leaves with scattered, multicellular, extremely long-headed hairs on abaxial surface, margin serrulate; corollas urceolate, 2–4.5 mm. long; calyx lobes 0.5–1.5 mm. long.

5. Inflorescences naked or with only few foliaceous bracts; [chiefly on mountains and Piedmont south of Virginia, and mountains, Piedmont, and Coastal Plain north of Virginia]. . . . . .6a. *L. ligustrina* var. *ligustrina.*

5. Inflorescences with conspicuously foliaceous bracts or at least lower inflorescences with large foliaceous bracts; [chiefly on Coastal Plain from southeastern Virginia to Florida, and west to eastern Texas, Oklahoma, and Arkansas (mountains)]. . . . . .6b. *L. ligustrina* var. *foliosiflora.*

4. Inflorescences fasciculate; leaves with scattered, multicellular, mostly short-headed hairs on abaxial surface, the margin entire; corollas ± cylindrical, 5–14 mm. long; calyx lobes 2–9.5 mm. long.

6. Leaves rigidly coriaceous, persistent, with intramarginal vein; corollas usually pink, swollen at base, 2–5 mm. wide; filaments merely roughened; capsules with apex at most slightly constricted. . . . . .8. *L. lucida.*

6. Leaves thinner, deciduous, lacking intramarginal vein; corollas usually white, not swollen at base, 4.5–9 mm. wide; filaments long-pubescent, especially near base; capsules with apex usually strongly constricted. . . . . .9. *L. mariana.*

Lyonia Nutt. sect. PIERIDOPSIS (Rehder) Airy Shaw, Curtis's Bot. Mag. **160:** *t. 9490.* 1937.

Pieris D. Don sect. *Eupieris* Bentham & Hooker, Gen. Pl. **2:** 588. 1876, *nomen illegit.*

Xolisma Raf. sect. *Pieridopsis* Rehder, Jour. Arnold Arb. **5:** 55. 1924. TYPE SPECIES: *Lyonia ovalifolia* (Wallich) Drude.

Deciduous to evergreen shrubs to trees, often spreading by horizontal underground rhizomes, the branches with homogeneous pith. Indumentum

of unicellular hairs and multicellular, biseriate-stalked, extremely long-headed hairs. Buds with 2 large, imbricate scales. Leaves entire, with unlignified or only slightly lignified epidermis and lacking hypodermis (except in *L. compta*); abaxial epidermis sometimes papillose and/or glaucous. Flowers in short to elongated racemes, 5-merous; calyx lobes valvate in bud; corolla cylindrical to urceolate; filaments with long, unicellular hairs, especially near base (rarely papillose), and unappendaged or with pair of small to very well developed spurs below junction with anthers. Capsules usually with pale, slightly to strongly thickened sutures, sutures usually adhering to valve or splitting irregularly in dehiscence, sometimes only poorly developed; placenta positioned subapically to centrally on columella; seeds oblong-ovoid to spindle shaped, one end sometimes truncated.

DISTRIBUTION. Asia, from northern Pakistan through Himalayas to western and central China, southern and central Japan, and Taiwan, extending southward into Vietnam, Cambodia, and Thailand, with disjunct populations in Malay Peninsula.

NUMBER OF SPECIES (TAXA). 5 (13).

1. **Lyonia compta** (W. W. Sm. & Jeffrey) Hand.-Mazz. Symb. Sin. **7:** 790. 1936.

Pieris compta W. W. Sm. & Jeffrey, Notes Roy. Bot. Gard. Edinburgh **9:** 116. 1916. *Xolisma compta* (W. W. Sm. & Jeffrey) Rehder, Jour. Arnold Arb. **5:** 53. 1924. TYPE: China, Yunnan, vicinity of Yun-nan-sen [Kun-ming Shih], in moist valleys, *E. E. Maire 1071* (lectotype, E!; isolectotypes, E!, K!, UC!).

Evergreen or nearly evergreen shrub to ca. 2 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to slightly angled, slender, with few long-headed hairs, otherwise sparsely to densely pubescent. Buds ovoid to elongate-ovoid, 1–4 by 1–2.5 mm. Leaf blades elliptic to obovate or sometimes ovate, 1.8–4.1 by 0.5–1.7(–2.2) cm., ± flat, coriaceous, ca. 0.23–0.34 mm. thick, apex acute to rounded with short mucro, base broadly cuneate to rounded (sometimes slightly cordate); margin entire, plane to clearly revolute; venation brochidodromous, 3° veins ± reticulate; adaxial surface with sparse long-headed hairs, otherwise ± glabrescent, sparsely to densely pubescent on midvein, both 2° and 3° veins obscure to only slightly visible; abaxial surface with sparse long-headed hairs, otherwise glabrous or sparsely pubescent on sides of midvein near leaf base, the 3° and higher order veins slightly and laxly reticulate, the 2° veins slightly raised and visible, ± irregular and sinuous, not much more prominent than 3° veins; petiole 1.5–5.5 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually above vegetative buds; inflorescences racemose, to ca. 35-flowered, (4.5–)6–15 cm. long, rigidly ascending; flowers not secund. Pedicels slender, 3–7 mm. long, with long-headed hairs, otherwise pubescent; bracteoles opposite, basal, triangular to ovate or linear, 0.8–1.8 mm. long; bracts large (often to 1 or 2 cm. long) and leaflike near base of raceme

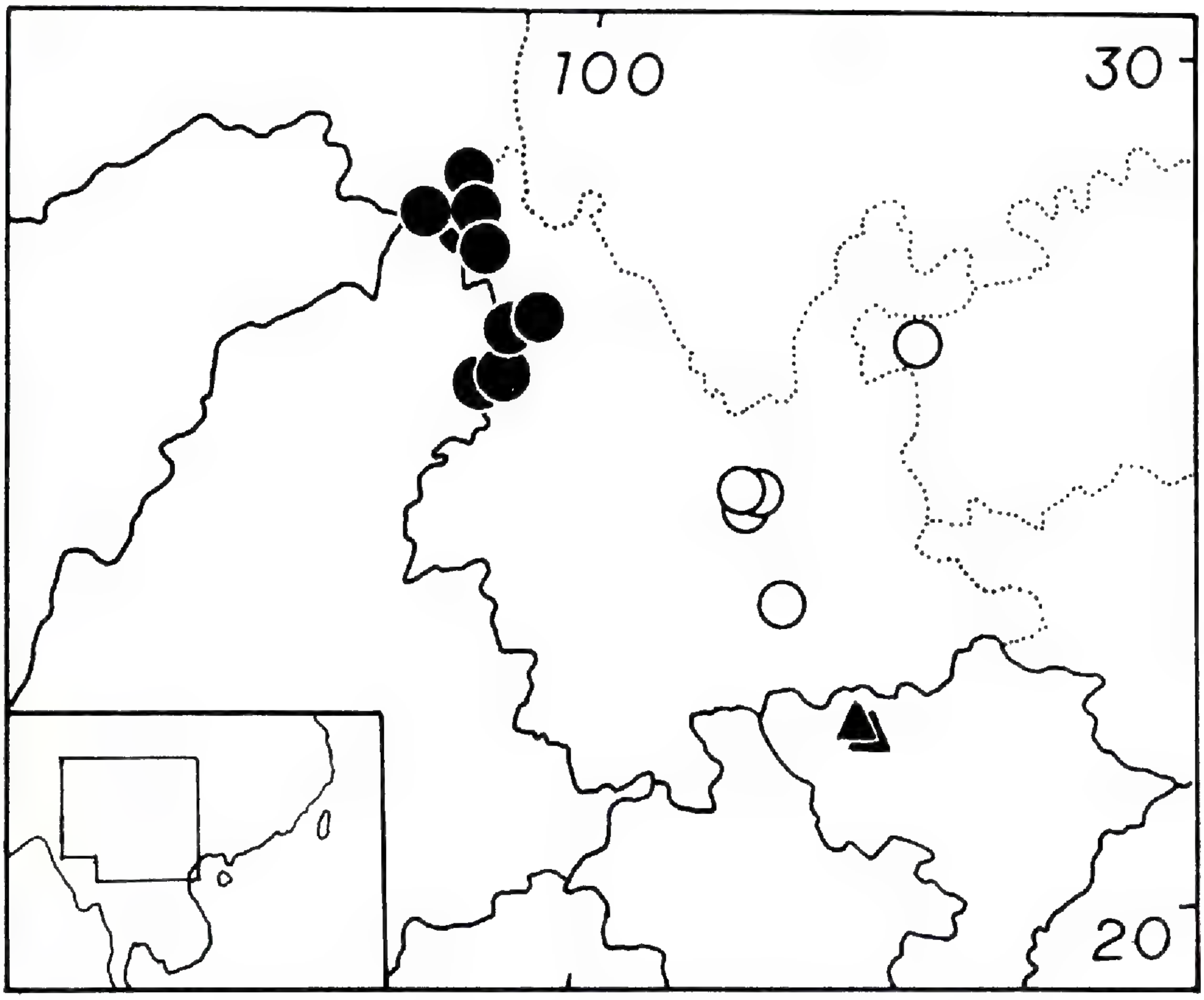
but near apex gradually becoming very small and similar to bracteoles. Flowers usually 5-merous; calyx lobes triangular to triangular-ovate, with acute to acuminate apices, 1–2(–2.4) by 0.7–1.7 mm., the adaxial side with few long-headed hairs near margins, sparsely pubescent near apex, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent, especially near base; corolla urceolate, 3–4.5(–5.5) by 2.7–4 mm., white, abaxially with moderate to dense long-headed hairs; filaments roughened in upper portion but always with at least few long, unicellular hairs often mixed with small papillae near base, 2–3.5 mm. long, with 2 ± well developed spurs to ca. 0.3 mm. long below anther-filament junction, anthers 1–1.5 mm. long; ovary pubescent, placentae subapical. Capsule short-ovoid or subglobose to globose, 2.7–4 by 3–4(–4.5) mm., ± lacking long-headed hairs, otherwise moderately to densely pubescent, especially near base, with pale, very poorly developed, at most slightly thickened sutures that in dehiscence split irregularly down middle with portions remaining attached to one or both adjacent valves; seeds 0.8–1.2 mm. long. (FIGURE 20; see also Stevens, 1970.)

DISTRIBUTION AND ECOLOGY. China, Yunnan and Kweichow provinces (MAP 5). Mountainous areas, open pine forests, moist valleys, marshy places, and savannas; over marl and sandstone; ca. 1400–2300 m. alt. (Handel-Mazzetti, 1936). Probably flowering chiefly late May through June.

REPRESENTATIVE SPECIMENS. **China.** KWEICHOW: locality illegible, *Esquirol 6062* (P). YUNNAN: Yunnan-fu to Tali-fu, Lufong, *Handel-Mazzetti 8657* (W); vic. of Yun-nan-sen, *Maire 1874* (E, UC, US); Lo Shuieh Mt., *McLaren's collectors U104* (A, E): Tsu-Gung, *McLaren's collectors 162F(aa)* (E, UC); Yunnan-fu Distr., Mt. Man-gan, *Schoch 145* (A, K, US); K'un-ming, *Wang 62680* (A).

Lyonia compta is a very distinctive species immediately recognizable by its more or less rigidly ascending racemes arising from buds toward the apices of the branches; small, urceolate corollas; usually short-ovoid capsules with only very poorly developed sutures; and usually quite small (to 4 by 1.7 cm.), elliptic to obovate leaves. It is also the only Asian species that has a hypodermis in its leaves. Although it clearly belongs in sect. PIERIDOPSIS, it is probably not closely related to any other Asian taxon. Its capsules are very similar to those of *L. chapaënsis*, but it differs from that species in its more strongly ascending, not secund inflorescences, which are more often leafy bracted and generally arise from floral buds situated above the vegetative buds on the branch. It also differs in its small, urceolate corollas; filaments more commonly with long, unicellular hairs near the base; shorter calyx lobes; and much smaller, differently shaped leaves with an adaxial hypodermis.

Several plants collected by Handel-Mazzetti near Yunnan-fu (*13085* (A, E, US, W)) have leaves that are longer than is normal for this taxon, with their secondary veins smoothly arching toward the leaf margin (vs. irregular or sinuous in typical *Lyonia compta*), and the tertiary veins more or less percurrent (vs. reticulate). The leaves also lack the adaxial hypodermis characteristic of *L. compta* but have a more or less discontinuous and slightly lignified layer of cells along their abaxial epidermis. The flowers have quite



MAP 5. Distribution of *Lyonia compta* (Yunnan and Kweichow; circles), *L. chapaënsis* (Vietnam; triangles), and *L. ovalifolia* var. *doyonensis* (Yunnan, Tibet, and Burma; dots).

large (to ca. 6 mm. long) corollas and elongate (to ca. 3.5 mm.), acute-tipped calyx lobes; they are borne on pedicels up to 10 mm. long. Finally, the bracts of the racemes do not decrease gradually in size from the base to the apex as is usual in *L. compta*; instead they often have only one to three large, foliaceous bracts near the base, with the other bracts very small and resembling the bracteoles in shape and size. All these characters tend toward the usual condition in *L. ovalifolia* var. *lanceolata,* which is sympatric with *L. compta.* These plants would be just as out of place in the former taxon because they show several features characteristic of *L. compta* (for example, corollas urceolate (vs. cylindrical and to ca. 12 mm. long in *L. ovalifolia* var. *lanceolata*), with a ± dense covering of long-headed, multicellular hairs; leaves coriaceous and evergreen, to ca. 4.5 mm. long, the apices obtuse to rounded with a small mucro (vs. usually ± deciduous, to ca. 11 cm. long, with acuminate apices); and inflorescences ± ascending, often arising near the apex of the branches (vs. ± horizontal to only slightly ascending, arising from floral buds that are generally below the vegetative buds)). It is probable that these morphologically intermediate specimens represent hybrids between *L. compta* and *L. ovalifolia* var. *lanceolata.*

Since Smith and Jeffrey (1916) did not select a type specimen for the species when it was described but merely listed two collections of E. E. Maire (nos. *1071* and *1874*), I have selected the specimen of *Maire 1071* at Edinburgh as the lectotype.

2. **Lyonia chapaënsis** (Dop) Merr. Jour. Arnold Arb. **23:** 188. 1942.

Pieris chapaënsis Dop in Lecomte, Fl. Gén. Indo-chine **2:** 726. 1930. TYPE: Tonkin [Vietnam], Massif de Lo-sui-tong, near Cha-pa, 2200 m. alt., 29 July 1926, *Poilane 12682* (holotype, P!; fragment of holotype, L!).

Pieris chapaënsis Dop var. *glabra* Dop & Trochain, Bull. Mus. Hist. Nat. Paris, ser. 2. **4:** 719. 1932. TYPE: Tonkin [Vietnam], Massif du Tam Dao, [Chapa], 1400 m. alt., May 1931, *Pételot 3214* (holotype, P!; isotypes, A!, NY (2 sheets)!, US (2 sheets)!).

Semi-evergreen shrub or small tree to ca. 4 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to slightly angled, slender, with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid to ovoid, 1–4 by 1–3 mm. Leaf blades elliptic to slightly obovate or ovate, 3.5–9.5 by 1.4–2.7 cm., ± flat, slightly coriaceous, ca. 0.12–0.24 mm. thick; apex acuminate to extremely long-acuminate and often curved; base narrowly cuneate to rounded; margin entire, plane to slightly revolute, usually irregularly undulate; venation eucamptodromous to slightly brochidodromous (especially toward apex), 3° veins reticulate to slightly percurrent; adaxial surface with sparse long-headed hairs, otherwise ± glabrescent, sparsely to densely pubescent on midvein and also sometimes on 2° veins, with 3° and higher order veins obscure to visible, not depressed to slightly so; abaxial surface with sparse long-headed hairs, otherwise glabrous or sparsely to moderately pubescent on sides of midvein near leaf base, occasionally with few hairs also on 2° veins, the 3° and higher order veins slightly visible, the 2° veins slightly raised and visible, smoothly arching toward margin; petiole 3–11 mm. long, with long-headed hairs, otherwise usually pubescent only adaxially. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 30-flowered, 4–10 cm. long, slightly (occasionally strongly) ascending; flowers pendulous and secund. Pedicels slender, 3–5 mm. long, with long-headed hairs, otherwise pubescent; bracteoles opposite, basal, narrowly triangular to linear, 1–2.6 mm. long; bracts often quite variable, all to ca. 2.5 mm. in length (or sometimes 1 to 3 leaflike ones to ca. 2.5 cm. long near base of raceme). Flowers 5-merous; calyx lobes triangular, with acute, slightly acuminate, or rounded apices, 2–2.7 by 0.6–0.8 mm., the adaxial side with few long-headed hairs (especially near margins), otherwise very sparsely to moderately pubescent, the abaxial side with scattered long-headed hairs, otherwise subglabrous; corolla long-urceolate, 4.5–5.5 by 3–4 mm., white, abaxially with sparse long-headed hairs; filaments roughened-papillose, lacking long-unicellular hairs or with few such hairs near base, ca. 3 mm. long, usually with 2 small spurs to ca. 0.2 mm. long below anther-filament junction, or unappendaged, anthers 1–1.2 mm. long; ovary pubescent, placentae ± subapical. Capsule short-ovoid to subglobose, 2.5–3

by 2.5–3.5 mm., lacking long-headed hairs, otherwise moderately to densely pubescent, with pale, at most very slightly thickened sutures that in dehiscence split irregularly down middle with portions remaining attached to one or both adjacent valves; seeds 1–1.2 mm. long. (FIGURE 20.)

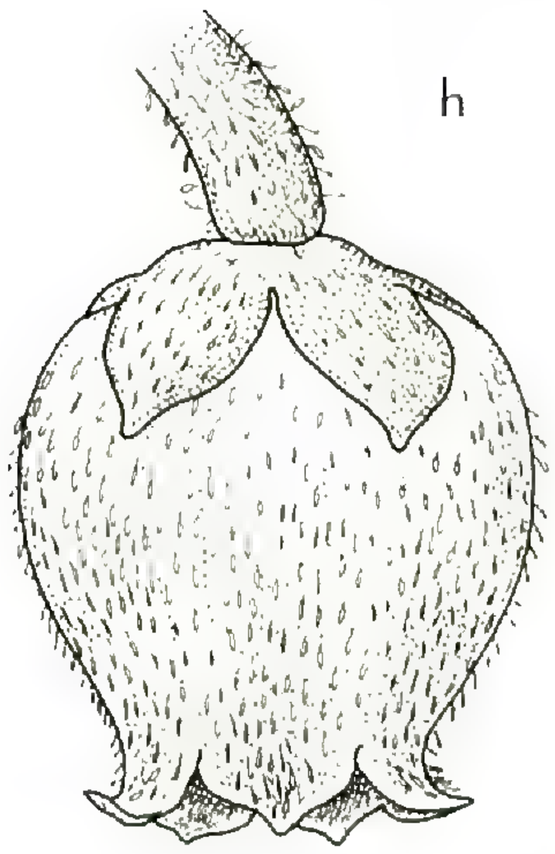
DISTRIBUTION AND ECOLOGY. Vietnam, vicinity of Cha-pa (MAP 5). Mountainous areas, ca. 1400–2200 m. alt. Single flowering specimen known to author (*Pételot 3214*) collected in May.

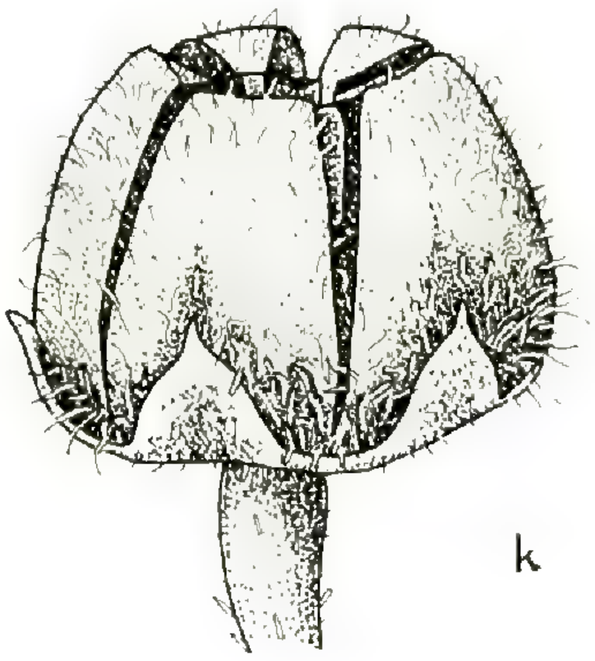
ADDITIONAL SPECIMENS EXAMINED. **Vietnam:** Massif du Fan tsi Pan, vic. of Cha-pa, *Pételot 4434* (NY, P).

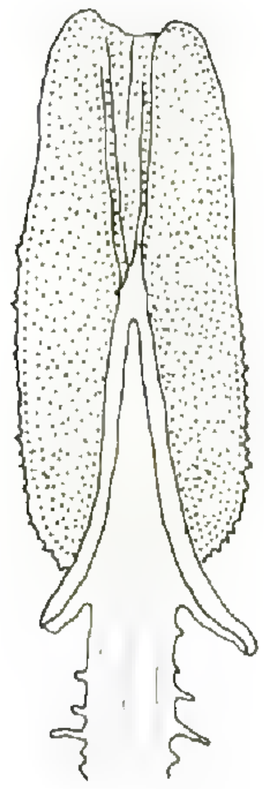
This interesting and narrowly endemic species is probably only distantly related to the other Asian taxa. It is easily distinguished by its leaves with their often extremely elongated, acuminate apices and slightly and irregularly undulate margins; by its often densely pubescent, short-ovoid capsules with very poorly developed suture thickenings; and by its roughened-papillose filaments that often lack unicellular hairs. *Lyonia chapaënsis,* especially if sterile, may be confused with *L. ovalifolia* vars. *lanceolata* or *rubrovenia* but can be recognized by its leaves, which usually have a distinctive shape and slightly undulate margins, and which lack a lignified layer (or layers) of mesophyll cells near the abaxial surface. Although its capsules are quite similar to those of *L. compta,* these two species differ in many other characters.

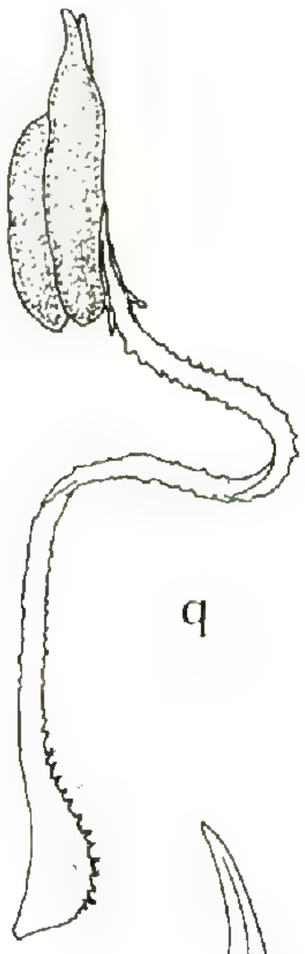
3. **Lyonia ovalifolia** (Wallich) Drude in Engler & Prantl, Nat. Pflanzenfam. **4**(1): 44. 1889.

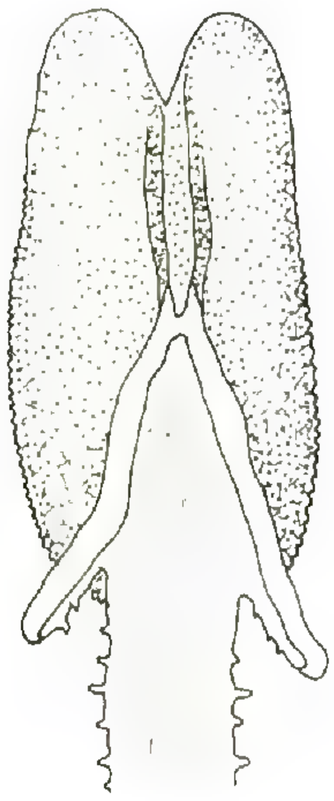
Deciduous to evergreen shrub to moderate-sized tree to 7.5(–18) meters tall, often with slightly twisted or gnarled trunk and brownish to gray, longitudinally furrowed bark, sometimes spreading vegetatively by horizontal underground rhizomes. Twigs terete or slightly ridged, slender to stout, often with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1–11.5 by 1–7 mm., often reddish. Leaf blades nearly orbicular, narrowly to widely elliptic, ovate, or obovate, 2.5–15(–21) by 0.8–10(–12) cm., ± flat, chartaceous to quite coriaceous, ca. 0.1–0.33 mm. thick, sometimes turning reddish in autumn, sometimes with 1 or 2 layers of lignified mesophyll cells near abaxial epidermis; apex long-acuminate to rounded with small mucro or obtuse, sometimes curved or folded over in pressing; base narrowly cuneate to cordate; margin entire, plane to slightly revolute; venation brochidodromous to eucamptodromous, 3° veins percurrent to reticulate; adaxial surface with sparse long-headed hairs, otherwise often glabrescent, very sparsely to densely pubescent on midvein, with pubescence sometimes extending to 2°, 3°, or higher order veins, occasionally all veins glabrous, the 3° and higher order veins visible to obscure, occasionally slightly depressed, the 2° veins prominently raised to slightly depressed or nearly obscure; abaxial surface papillose to smooth, glaucous or greenish to shiny yellowish gold, with sparse to dense long-headed hairs, otherwise glabrous or very sparsely to densely pubescent along midvein, with pubescence occasionally extending to adjacent 2° or higher order veins, the 3° and higher order veins visible to obscure,

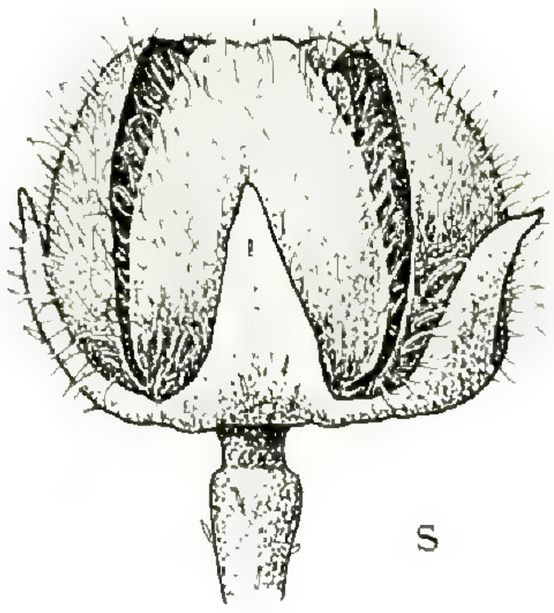












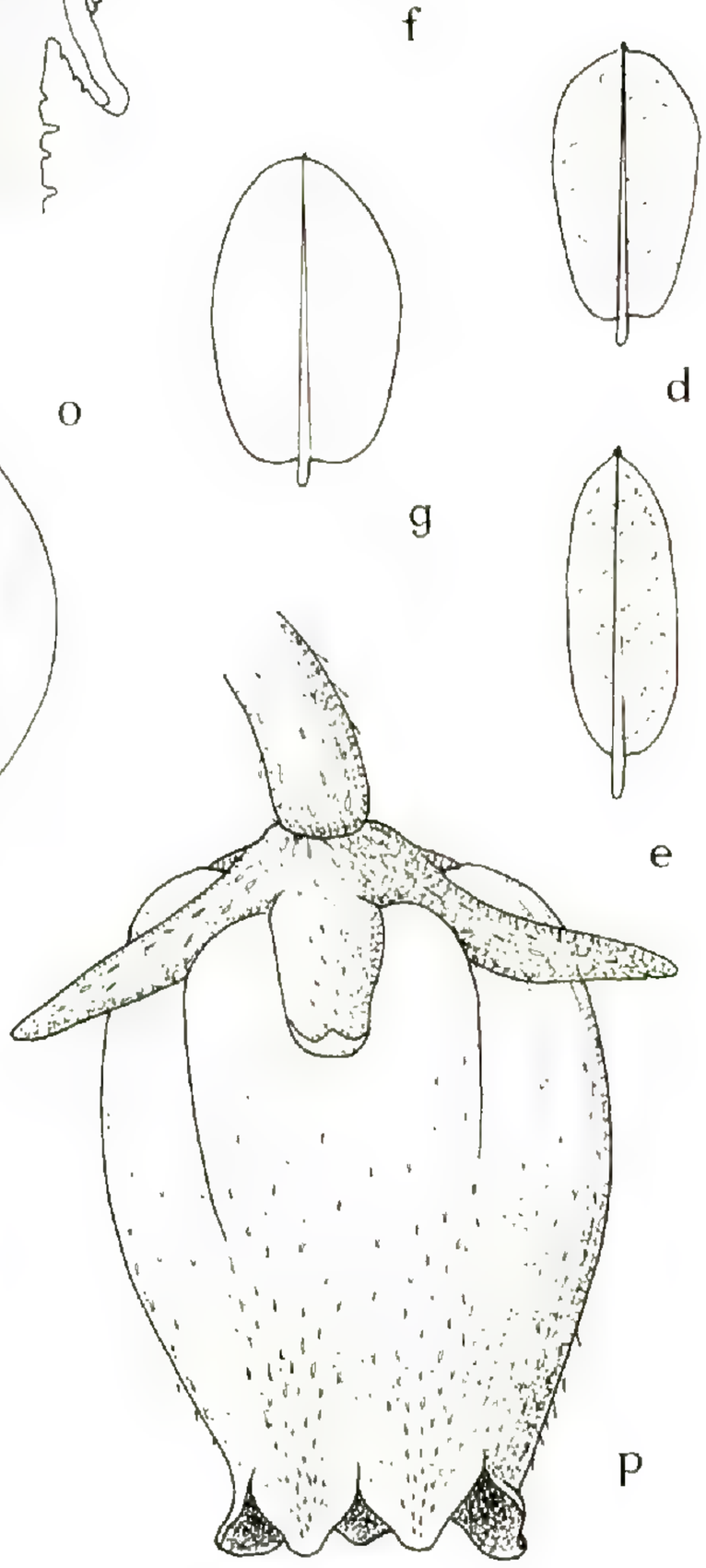


FIGURE 20. a–k, *Lyonia compta:* a–g, leaves, × .5; h, flower, × 6; i, stamen, × 12.5; j, anther, × 25; k, capsule, × 6. l–s, *L. chapaënsis:* l–o, leaves, × .5; p, flower, × 6; q, stamen, × 12.5; r, anther, × 25; s, capsule, × 6.

the 2° veins prominently raised and visible to nearly obscure, smoothly arching toward margin to sinuous or irregular and joined together to form series of arches, occasionally drying slightly ferrugineous; petiole 2–15(–20) mm. long, with long-headed hairs, otherwise glabrous or pubescent adaxially or all around. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 40- (to 60-)flowered, (1.5–)2–16(–30) cm. long, horizontal to slightly ascending; flowers pendulous and secund. Pedicels slender to stout, (1.5–)2–10 mm. long, with long-headed hairs, otherwise glabrous or ± pubescent; bracteoles opposite, basal, widely triangular to linear, 0.4–2.5(–4) mm. long; bracts extremely variable, 1 to 9 large and leaflike near base of raceme, the others very small, similar to bracteoles in shape, often caducous (occasionally all small and similar to bracteoles in shape). Flowers 5-merous; calyx lobes triangular to nearly linear, with acuminate or acute to rounded apices, 1–5(–6.5) by 0.6–1.9(–2.5) mm., the adaxial side often with few long-headed hairs, otherwise glabrous to densely pubescent, the abaxial side with scattered long-headed hairs, otherwise glabrous or sparsely (rarely densely) pubescent; corolla cylindrical to slightly urceolate, 5–13(–13.5) by 2.5–6.5(–7) mm., white or sometimes slightly pink tinged, especially toward apex, abaxially with sparse to dense long-headed hairs; filaments with long-unicellular hairs, especially near base, 3–9 mm. long, with 2 spurs to ca. 0.2–0.5 mm. long below anther-filament junction, anthers 0.8–1.8 mm. long; ovary glabrous to densely pubescent, placentae subapical to central. Capsule subglobose, globose, short-ovoid, or ovoid, 2.5–5.5 by 2.5–6 mm., very occasionally with few long-headed hairs, otherwise glabrous to densely pubescent, especially near base, with pale, moderately (sometimes only slightly) thickened sutures that in dehiscence usually remain attached to an adjacent valve or split irregularly; seeds 0.7–1.6 mm. long.

DISTRIBUTION. In an arc from Japan westward across China (including Taiwan and Hainan) to northern Pakistan, south to Thailand and Malay Peninsula. Various habitats, 20–3350(–3800) m. alt.

Key to the Varieties of *Lyonia ovalifolia*

1. Secondary veins often slightly sinuous, of varying strengths and angles of divergence from midvein, the connections between secondary veins often clearly visible.
   2. Abaxial leaf surface densely pubescent along secondary veins and sides of midvein, always with dense tuft of long-unicellular hairs in angle between midvein and secondary veins at leaf base; inflorescences (1.5–)2–7(–10) cm. long; corollas 6–8(–9.5) mm. long; leaves 3.5–10.5(–13) cm. long; [Japan and Taiwan]. . . . . 3a. var. *elliptica*.
2. Abaxial leaf surface glabrous to sparsely or densely short-pubescent along secondary veins and midvein, but never with such a tuft of hairs; inflorescences 3–13(–20) cm. long; corollas 6.5–12.5 mm. long; leaves 5–12.5(–16) cm. long; [China].
   3. Leaves longer than wide, 5–12.5(–15) by 2.3–6.5(–8) cm., length/width ratio (1.6–)1.8–3(–3.5), apex usually acuminate to long-acuminate, base obtuse to cordate, blade usually chartaceous to slightly coriaceous, abaxial epidermis not papillose; inflorescence axis glabrous

to sparsely pubescent; [Kiangsu and Chekiang west to Szechwan and Yunnan, south to Kwangsi and Kwangtung] . . . . . 3b. var. *hebecarpa*.

3. Leaves as wide as long or nearly so, 6.5–12(–16) by 5.3–10(–12) cm., length/width ratio 0.9–1.3(–1.5), apex abruptly short-acuminate, base rounded to cordate, blade usually quite coriaceous, abaxial epidermis obscurely to clearly papillose; inflorescence axis glabrous; [northwestern Yunnan and adjacent Tibet and Burma] . . . . . 3c. var. *doyonensis*.

1. Secondary veins smoothly arching toward leaf margin (to rarely slightly irregular in var. *ovalifolia*), their interconnections often obscure.
   4. Leaves quite large and as wide as long or nearly so, 6.5–12(–16) by 5.3–10(–12) cm., length/width ratio 0.9–1.3(–1.5), apex truncately short-acuminate, abaxial side with tertiary veins very prominent and epidermis papillose; [northwestern Yunnan and adjacent Tibet and Burma] . . . . . 3c. var. *doyonensis*.
   4. Leaves without above character combination, usually much longer than wide, 2.5–15(–21) by 1–8.5(–11.5) cm., length/width ratio (1.2–)1.4–7, apex long- to short-acuminate, acute, or obtuse, abaxial side with tertiary veins obscure to visible but not prominently raised, and with epidermis often lacking papillae.
      5. Leaves usually ovate, with base widely cuneate to rounded or cordate, blade 6–15(–21) by (2–)3.5–8.5(–11.5) cm., length/width ratio (1.2–)1.4–2.4(–2.5), the abaxial epidermis green to glaucous, sometimes papillose, only occasionally yellowish and shiny when dried; capsules usually subglobose; calyx lobes 1.5–2.5 mm. long (but to ca. 3.5 mm. in western Himalayas); inflorescences 3–16(–30) cm. long; lamina with mesophyll cells never lignified; [Pakistan and northwestern India east to Yunnan and Kwangsi, south to Thailand and Malay Peninsula] . . . . . 3d. var. *ovalifolia*.
      5. Leaves elliptic to obovate or ovate, with base usually narrowly cuneate to rounded, blade 2.5–11(–14.5) by 1.2–4.5(–7) cm., length/width ratio (1.5–)1.7–3.5(–7), abaxial epidermis greenish to yellowish green and lustrous when dried, never papillose or glaucous; capsules often short-ovoid to ovoid, less commonly globose to subglobose; calyx lobes (2–)2.5–4.5(–6.5) mm. long; inflorescences 2.5–9(–18) cm. long; lamina with 1 or 2 layers of lignified mesophyll cells near abaxial epidermis.
         6. Capsules subglobose to globose, sutures often poorly differentiated from valves; corollas 5–7 mm. long; filaments 3–4 mm. long with spurs 0.1–0.3 mm. long; inflorescences usually lacking foliaceous bracts; [Hainan and Vietnam] . . . . . 3g. var. *rubrovenia*.
         6. Capsules ovoid to short-ovoid, less commonly globose (or subglobose), sutures usually well differentiated from valves; corollas (6–)7–10(–12.5) mm. long; filaments 5–7.5 mm. long with spurs 0.2–0.6 mm. long; inflorescences with at least few large, foliaceous bracts near base.
            7. Leaves 2.5–6(–7) cm. long, apex abruptly short-acuminate, to obtuse or rounded with small mucro, petiole 2–8 mm. long; inflorescences with foliaceous bracts often ± throughout; capsules 2.5–4 mm. long; [Thailand] . . . . . 3f. var. *foliosa*.
            7. Leaves 5–11(–14.5) cm. long, apex acuminate, petiole 5.5–14

mm. long; inflorescences with foliaceous bracts usually limited to base; capsules 3–5(–5.5) mm. long; [China and northern Burma] . . . . . 3e. var. *lanceolata.*

3a. **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz. Symb. Sin. 7(4): 788. 1936.

Andromeda elliptica Sieb. & Zucc. Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München **4:** 126. 1846. *Pieris ovalifolia* (Wallich) D. Don var. *elliptica* (Sieb. & Zucc.) Rehder & Wilson in Sarg. Pl. Wilson. **1:** 552. 1913. *Pieris elliptica* (Sieb. & Zucc.) Nakai, Tokyo Bot. Mag. **33:** 207. 1919. *Xolisma ovalifolia* (Wallich) Rehder var. *elliptica* (Sieb. & Zucc.) Rehder, Jour. Arnold Arb. **5:** 52. 1924. *Xolisma elliptica* (Sieb. & Zucc.) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927, non Wright ex Small, 1914. *Lyonia neziki* Nakai & Hara, Jour. Jap. Bot. **14:** 336. 1938, *nomen novum. Lyonia ovalifolia* subsp. *neziki* (Nakai & Hara) Hara, Fl. East. Himalaya, 648. 1966. TYPE: Japan, locality not specified. Lectotype should be selected from material sent to Siebold by H. Bürger in 1842, and labeled as "Andromeda (Pieris) elliptica S. & Z. . . . no. 433" at L, but material at LE must be examined; specimens at L, M, and K seen.

Pieris formosana Komatsu in Matsum. Ic. Pl. Koishikav. **3:** 71. *t. 181.* 1916. *Xolisma formosana* (Komatsu) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927. TYPE: Taiwan, Ren-tai-san, *Hayata & Mori s.n.*, 10 Aug. 1908 (lectotype, TI!).

Pieris pilosa Komatsu in Matsum. Ic. Pl. Koishikav. **3:** 73. *t. 182.* 1916. *Xolisma formosana* (Komatsu) Nakai var. *pilosa* (Komatsu) Nakai, Trees Shrubs Japan. ed. 1 (rev.). 204. 1927. TYPE: Taiwan, not seen.

Deciduous shrub to small tree to 6(–12) meters tall. Buds 1–9 by 1–3.5 mm. Leaf blades elliptic, ovate, or less commonly obovate, 3.5–10.5(–13) by 1.8–6(–7.5) cm., mesophyll unlignified; apex acute to long-acuminate, sometimes curved, often folded over in pressing; base cuneate, or rounded to cordate; venation brochidodromous, 2° veins sinuous or irregular; abaxial surface neither papillose nor glaucous, densely pubescent along 2° veins and sides of midvein, to almost glabrous, always with dense tuft of long-unicellular hairs along sides of midvein and adjacent 2° veins at leaf base; petiole 4.5–18 mm. long. Inflorescences (1.5–)2–7(–10) cm. long, usually with ca. 1 to 3 large, leaflike bracts to 2–6(–11) cm. long near base. Calyx lobes 1–3.5(–4) by 0.6–1.5 mm.; corolla cylindrical, 6–8(–9.5) by 2.5–4.5(–5.5) mm.; filaments 3–5.5 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule subglobose to globose or less commonly short-ovoid, 2.5–4.5 by 3–4.5 mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 21; see also Okuyama (1959) and Makino (1961) for drawings based upon Japanese material, and Matsumura (1916), Kanehira (1936), Liu (1962), and Li (1963) for drawings from Taiwanese material.)

DISTRIBUTION. Japan (chiefly western and southern Honshu, Kyushu, and Shikoku) and Taiwan (MAP 6; see also Horikawa, 1975).

ECOLOGY. Temperate to warm-temperate regions; *Tsuga sieboldii–Cleyera*

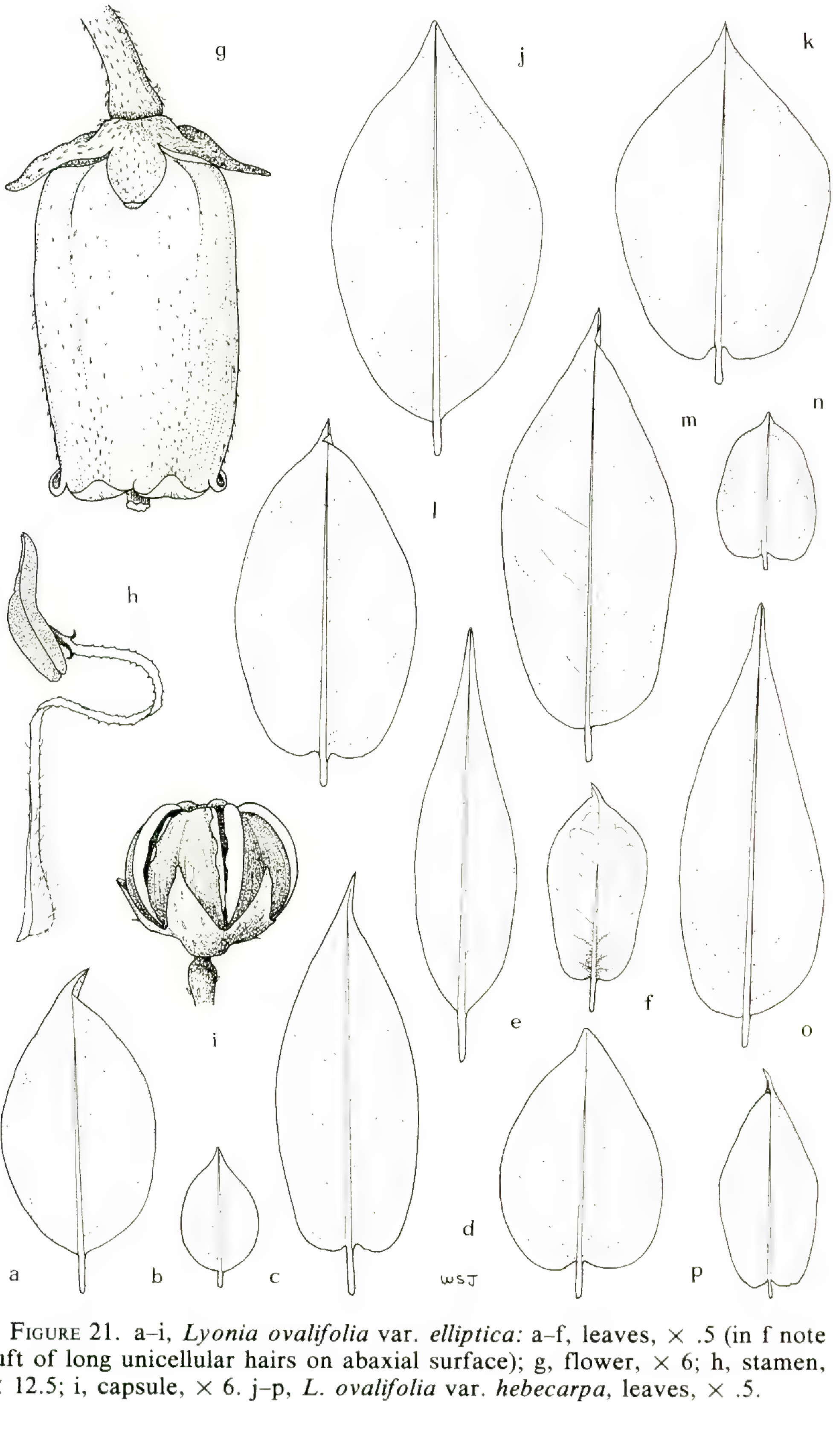
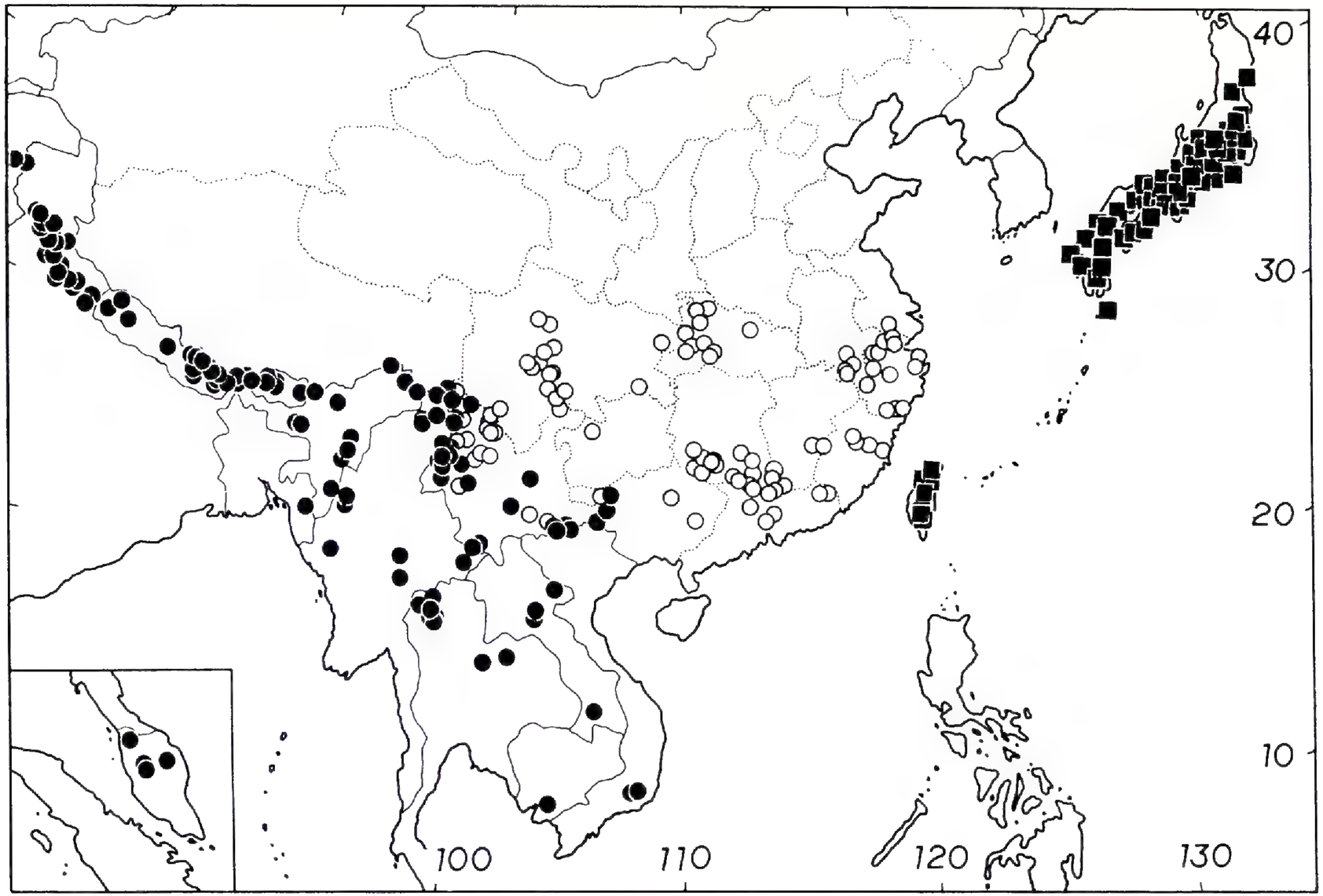


FIGURE 21. a–i, *Lyonia ovalifolia* var. *elliptica:* a–f, leaves, × .5 (in f note tuft of long unicellular hairs on abaxial surface); g, flower, × 6; h, stamen, × 12.5; i, capsule, × 6. j–p, *L. ovalifolia* var. *hebecarpa,* leaves, × .5.



MAP 6. Distribution of *Lyonia ovalifolia* var. *elliptica* (squares), *L. ovalifolia* var. *hebecarpa* (circles), and *L. ovalifolia* var. *ovalifolia* (dots).

japonica–Symplocos myrtacea forests, *Castanopsis cuspidata–Cleyera japonica* forests, *Castanopsis cuspidata–Rapanaea neriifolia* forests, *Tsuga sieboldii–Pseudotsuga japonica* forests, *Fagus crenata* forests, thickets, mountain ridges, grasslands, dry sunny slopes, forest margins, and near hot springs; 1800–2700 m. alt. See Tatewaki & Misumi (1957) and Yatoh (1960) for characteristic species of the above-mentioned forest types. In Japan flowering chiefly late May through July (varying with elevation, latitude, season); on Taiwan as early as April in some areas, extending through July.

COMMON NAMES. Nejiki or neziki (Japan); seiban-nejiki or Taiwan-nejiki (Taiwan).

REPRESENTATIVE SPECIMENS. **Taiwan:** Yang-min-shan, Taipei Hsien, *Chen s.n.*, 28 March 1959 (TAI); Ari-san, *Faurie 172* (A); near sulfur hot springs, Taipeh, *Faurie 294* (P, UC, W); Chu-shan, Chiayi Hsien, *Hsu & Chuma 8928* (TAI); Mt. Ho-huan to Mt. Lee-shan, Tai-chung Hsien, *Huang 4679* (TAI); Mt. Stone, Kao-hsiung, *Huang 6510* (TAI); Ta-pa-chien-shan, Hsin-chu Hsien, *Kouh 3817* (TAI); Mt. Housha-shan, Hwaling, *Liu & Liu 180* (TAI); Mt. A-li, Ohia-yi Hsien, *Liu 337* (A); Mt. Nanhuta-shan, Ilan Hsien, *Tamura & Shimizu 20599* (E, S); Sozan, Taihoku Hsien, *Wilson 10771* (A, K, US); Ari-san to Mt. Morrison, *Wilson 10942* (A, US); Tsuei-fung to Sung-kang, Nantou Hsien, *Wu, Leu, & Chiu 7706* (TAI). **Japan.** CENTRAL HONSHU: Aichi pref., Mt. Hooraiji, Minamishidara-gun, *Kanai 6870* (A, TAI, TI); Awaji prov., Sumoto Is., *Murai 3024* (A); Echigo prov., Niigata-ken, Mt. Komagatake, *Nakamura s.n.*, 31 Aug. 1905 (TNS); Echizen prov., Itoo-mura, *Maeda 10466* (A); Fukui pref., Tsuruga-city, Yamanaka, *Hasegawa s.n.*, 30 June 1968 (TI); Gifu pref., Do, Sakashita-mura, Yoshiki-gun, *Kanai 6309* (TAI); Gumma prov., Nishikurozawa, Mt. Tanikawa, *Suzuki 69* (A); Hida prov., *Tomioku 5976* (A); Hitachi prov., Mt. Tsukuba, *Kobayashi 3020* (A, S); Hyogo pref., Mt. Rokko, *Hiroe 14067* (UC); Ise prov., Mie-ken, Takami Pass, *Sakurai s.n.*, May 1888 (TNS); Kai prov., Yamanashi-ken, Mt. Mitsutoge, *Hiyama 5149* (KAI, TNS); Kyoto pref., Mt. Arashiyama, W. of Kyoto-city, *Hiroe 13972* (UC); Mikawa prov., Tsugeno, *Kitamura s.n.*, 26 July 1952 (A); Mino prov., *Ito 7916* (A); Musashi prov., Kori-mura, Nishitama-gun, *Mizushima 2324* (A); Nagano pref., Hara-mura, Suwa-gun, *Kanai 6311* (A, TI); Nara pref., Mt. Omine, Yoshino-gun, *Shimizu 4375* (S); Osaka pref., Tannowa, *Muroi 6753* (A); Owari prov., *Kato 8776* (A); Settsu prov., Yamamoto, *Togasi T.N.S. 1503* (A, K, MAK, TNS, UC, W); Shiga pref., Mt. Uchimi, Shiga-gun, *Kitamura & Murata 2371* (MAK); Shimotsuke prov., Jakkotaki trail, Nikko, *Mizushima 2282* (A); Shinano prov., Narai, *Jack s.n.*, 3 Sept. 1905 (A); Tochigi pref., Kuroiso-cho, *Ide s.n.*, 16 June 1940 (TNS); Tokyo pref., Murayama reservoir, *Kanai 6310* (TAI); Totomi prov., Aratama-mura, Inasa-gun, Shizuoka pref., *Furuse s.n.*, 11 Oct. 1960 (S); Yamashiro prov., Mt. Daimonji, *Kitamura s.n.*, 20 Sept. 1936 (A). NORTHERN HONSHU: Fukushima pref., Omotego-mura, Nishishirakawa-gun, *Makino Herb. 81385* (MAK); Rikuzen prov., Akiu, *Ohashi 3053* (TI); Uzen prov., Yamagata-ken, Yonezawa, *Matsushima T.N.S. 37101* (TNS). WESTERN HONSHU: Bizen prov., *Masamune s.n.*, 7 Oct. 1925 (NY); Okayama pref., Mituisi, *Muroi 4810* (A); Suo prov., Mt. Gabi, Murozumi, *Migo s.n.*, 13 July 1954 (A); Yamaguchi pref., 2.5 mi. SW. of Yokoyama, Iwahuni-city, *Charette 1723* (S, UC). KYUSHU: Bungo prov., Beppu, *Ishidoya s.n.*, Aug. 1917 (A); Fukuoka pref., Hakozaki, near Fukyoka-city, *Ichikawa 22* (A, W); Hizen prov., Nagasaki, *Faurie 3441*

(P); Miyazaki pref., Obi, *Hattori s.n.*, 26 May 1948 (S); Osumi prov., Mt. Takakuma, *Kawagoe s.n.*, 9 Nov. 1917 (A); Tanegashima Is., *Yano s.n.*, 31 July 1964 (MAK). SHIKOKU: Iyo prov., Hiroshima, *Togashi s.n.*, 11 May 1961 (TI); Tokushima pref., Mt. Otaki, Mima-gun, *Makino Herb. 105379* (MAK); Tosa prov., Takeyashiki, *Watanabe s.n.*, 13 June 1887 (UC).

3b. **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun, Sunyatsenia **4:** 253. 1940.

Pieris ovalifolia (Wallich) D. Don var. *hebecarpa* Franchet ex Forbes & Hemsley, Jour. Linn. Soc. Bot. **26:** 17. 1889. *Xolisma ovalifolia* (Wallich) Rehder var. *hebecarpa* (Franchet ex Forbes & Hemsley) Metcalf, Jour. Arnold Arb. **12:** 275. 1931. TYPE: China, prov. Chekiang, Meichi, *Poli s.n.* (not seen).

Pieris henryi Lévl. Bull. Soc. Bot. France **53:** 204. 1906. TYPE: China, prov. Yunnan, Mengtze, mountains, 6500 ft. alt., *A. Henry 9681* (holotype, E!; fragment of holotype, A!).

Pieris mairei Lévl. Bull. Acad. Int. Géogr. Bot. **25:** 21. 1915. TYPE: China, prov. Yunnan, collines calcaires de Tcha-Ho, 2600 m. alt., July 1912, *E. E. Maire s.n.* (holotype, E!; fragment of holotype, A!; isotype, E!).

Pieris mairei Lévl. var. *parvifolia* Lévl. Bull. Acad. Int. Géogr. Bot. **25:** 21. 1915. TYPE: China, prov. Yunnan, collines arides de Tche-Hai, 2500 m. alt., June 1912, *E. E. Maire s.n.* (holotype, E!; fragment of holotype, A!).

Deciduous shrub to moderate-sized tree to 5(–15) meters tall. Buds 1–11.5 by 1–4.5 mm. Leaf blades ovate, obovate, or elliptic, 5–12.5(–15) by 2.3–6(–8) cm., mesophyll unlignified; apex acuminate to long-acuminate, often folded over in pressing; base rounded to cordate; venation brochidodromous, 2° veins sinuous or irregular; abaxial surface not papillose, glaucous or green, glabrous or sparsely pubescent along proximal portion of midvein, never with dense tuft of long-unicellular hairs at leaf base; petiole 3–14 mm. long. Inflorescences (2.5–)3.5–13(–16) cm. long, usually with 1 to 4 large, leaflike bracts to 2.5–6(–9) cm. long near base. Calyx lobes 1–2.5(–3) by 0.6–1.5 mm.; corolla cylindrical, 6.5–11.5 by 2.5–6.5 mm.; filaments 4–6.5 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule globose to subglobose or short-ovoid, 2.5–4 by 2.5–4 mm., with 5 pale, thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 21; see also Fang, 1944, labeled as *Lyonia ovalifolia* var. *elliptica*, and Anonymous, 1974a.)

DISTRIBUTION. China, Kiangsu and Anhwei west to Szechwan and Yunnan, south to Kwangsi and Kwangtung (MAP 6).

ECOLOGY. Both cold- and warm-temperate areas; open pine and oak forests, forest margins, thickets, meadows, dry and/or rocky slopes, often along streams; ca. 120–3300(–3800) m. alt. in Yunnan and Szechwan provinces, 2300 m. or less elsewhere. Flowering May through early August, usually peaking June or July.

REPRESENTATIVE SPECIMENS. **China.** KIANGSU: I-Hsing, Lungche Mt., *Keng 2460* (A). ANHWEI: Wang-che, S. Chu-hwa shan, *Ching 2838* (A, E, K, UC); Wu

Yuen, *Ling 1315* (UC); Wang Shan, above Tiao Ch'tao, *Steward 1250* (A, E, UC). CHEKIANG: Mokan Shan, *Cheo & Wilson 42* (GH, UC); Sze-ton, S. of Siachu, *Ching 1693* (A, UC, W); W. of Wenchow, *Ching 1843* (A, E, GH, UC, US); Ping Ying, toward Tai Suan, *Ching 2094* (A, K, US, W); Tein-mu Shan, *Ching 6184* (A, E, UC); Chun-an Hsien, *Keng 675* (A, UC); Chang-shan Hsien, *Keng 832* (A, UC); Tung-yang Hsien, *Keng 934* (A, UC); Mei-chi, An-chi Hsien, *Liu & Ching 4928* (A, E, K, UC); near Ningpo, *Macgregor s.n., 1908* (A); Han-chow, *Meyer 396* (A). KIANGSI: Shui-shueng Hsien, *Hsiung 5525* (A); Ta Yu Hsien, *Hu 970* (A); Ningdu near Yuanhsiang-schi, *Hui 360* (A, E, W); Kiennan distr., Sai Hang Cheung, *Lau 4321* (A, S, US); Lungnan distr., Oo Chi Shan, *Lau 4403* (A, S, US). FUKIEN: Yenping, Chi-yuan-keng bat cave, *Chung 2980* (A, E, K, UC, W); Kuliang, *Chung 6618* (A, F); Kutien, *Chung's coll. 4034* (A). KWANGTUNG: Canton, *Carles s.n.*, March 1877 (E); NW. Kwangtung near Hunan border, Gantung, *Fenzel 71* (UC); S. of Mei Hsien, Tsin Leong San, *Gressitt 1237* (A, E, UC); Yu-yuen, *Ko 52711* (A); Wung Yuen distr., Tsing Wan Shan, *Lau 2073* (A); Luang-lin, Ta-pu, *Schindler 437c* (K); Lung T'au Mt., near Iu, *To & Tsang 361, C.C.C. 12360* (E, S, UC, W); Sam Kok Shan, Tsungfa and Lungmoon, *Tsang 20541* (US, W); Yao Shan, Lokchong, *Tso 20766* (E); Ying-tak distr., *Wang 549* (A, W). HUPEH: Tzu-kwei Hsien, *Chow 373* (A, E); Huan Tsan, *Chun 4104* (A); Chien-shih, *Henry 5806a* (A, E, GH, K, US); Ou-tan-scian, *Silvestri 3127* (A); I-chang, *Wilson 492* (A, E, GH, W); Chang-yang Hsien, *Wilson 3189* (A, E, GH, K, W); Fang Hsien, *Wilson 3188* (A, E, GH, W); Patung Hsien, *Wilson 492a* (A). HUNAN: Tienchaosan, *Dahlstrom 272* (S); Yang Shan, Changning Hsien, *Fan & Li 203* (A, L, W); Sinning Hsien, Ma-Ling-Tung, *Fan & Li 455* (A, L, W); near Wukang, *Handel-Mazzetti 11995* (A, E, W). KWEICHOW: Ku-kai Shan, Tating, *Tsiang 8836* (E, S, UC). KWANGSI: Bin Long, Min Shan, N. Luchen, *Ching 6040* (A, W); Shing-An Hsien, Ssn-Men-Chien, Tu-Ti-Tang, *Chung 81803* (A); Tzu Yuen distr., *Chung 83519* (A); Pai-yun-an, Ch'uan distr., *Tsang 27225* (A); Ling-ch'uan distr., Ta-ling, *Tsang 27895* (A, UC). SZECHWAN: Omei Shan, *Chiao & Fan 163* (A); Po-shin Hsien, *Chu 2975* (A, E, K); Po-shin, *Chu 3669* (A, E); Chin-fu Shan, Nan-chuan Hsien, *Fang 601* (A); Kuan Hsien, *Fang 2095* (A, E); Luting Hsien, *Fang 3229* (A, E); Wen-chuan Hsien, Tsao-puh, *Hu 2301* (A); Wan Hsien, Mon-tao-chi, Shih-men-pa, *Hwa 73* (A, UC); Mt. Tien-chuan, *Liu 1336* (A); near Tachienlu, *Pratt 279* (K, P); S. of Muli, *Rock 16127* (A, E, US); Opien Hsien, *Sun 943* (US); SE. of Mao Hsien, *Wang 21975* (A); Wu-shan, *Wilson 1157* (A, E, GH, W); Mo-pin, *Wilson 3190* (A, E, W); Ping-shan Hsien, *Yü 3111* (E); Lei-po Hsien, *Yü 3346* (E). YUNNAN: W. Likiang, Ta-mi-chung, *Ching 21588* (A); E. flank of Tali Range, 25°40′N., *Forrest 4180* (A, E, K); hills forming E. boundary of Lichiang Valley, 27°25′N., *Forrest 6112* (E); Lichiang Range, 27°40′N., *Forrest 10172* (A, E, K); Mekong-Salwin divide, 27°54′N., 98°50′E., *Forrest 19647* (A, E, K, UC, W); ranges S. of Yung-chang-fu Valley, 24°50′N., 99°20′E., *Forrest 24349* (E, K); Tché-hai, *Maire* (A); Tsekou, *Soulier 1376* (F); Yung-shan Hsien, *Tsai 51118* (A); Pin-chuan Hsien, *Tsai 52976* (A); Shih-ping Hsien to Ping Shan, *Tsai 53352* (E); Ta-li Hsien, *Tsai 53826a* (A, E); Lan-ping Hsien, *Tsai 56268* (A); Wei-se Hsien, *Tsai 57861* (A); Huan-fu-ping, *Wang 69334* (A).

3c. **Lyonia ovalifolia** (Wallich) Drude var. **doyonensis** (Hand.-Mazz.) Judd, comb. et stat. nov.

Pieris doyonensis Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. **60:** 185. 1923. *Lyonia doyonensis* (Hand.-Mazz.) Hand.-Mazz. Symb. Sin. **7:** 789. 1936. TYPE: China, prov. Yunnan, Doyon-lumba Valley near Lu-djiang (Salween), 28°2′N., 2700–2900 m. alt., *Handel-Mazzetti 9600* (holotype, w!; fragment of holotype, A!; isotypes, A!, E!).

More or less deciduous shrub to moderate-sized tree to 5(–12) meters tall. Buds 1–11 by 1–7 mm. Leaf blades nearly orbicular to widely obovate or ovate, (4–)6–12(–16) by 5.3–10(–12) cm.; mesophyll unlignified; apex usually truncately short-acuminate; base rounded to cordate; venation ± brochidodromous, 2° veins smoothly arching toward margin to slightly irregular or sinuous; abaxial surface obscurely to clearly papillose, glaucous or green, glabrous; petiole 7–15 mm. long. Inflorescences (5–)6–12(–20) cm. long, usually with ca. 1 to 3 large, leaflike bracts to 3–7.5 cm. long near base. Calyx lobes 1.7–2.7 by 0.9–1.8 mm.; corolla cylindrical, 9–13 by 3.5–6.5 mm.; filaments 4–7 mm. long, with 2 spurs to ca. 0.4 mm. long. Capsule ± subglobose, 3–3.5 by 3.5–5 mm., with 5 pale, quite thickened sutures that in dehiscence usually remain attached to an adjacent valve. (FIGURE 22; see also Anonymous, 1974a.)

DISTRIBUTION AND ECOLOGY. Northwestern Yunnan (China) and adjacent areas of northern Burma and extreme southeastern Tibet (MAP 5). Pine forest, open woods, wooded ravines and slopes, thickets, along river banks; ca. (2000–)2400–3350 m. alt. Flowering chiefly June through early August.

REPRESENTATIVE SPECIMENS. **China.** YUNNAN: Wei Hsi, *McLaren's collectors D177* (A, E); Chih-tse-lo, *Tsai 54118* (A, PE); Shang-pa Hsien, *Tsai 54456* (A, PE); Upper Kiukiang Valley, (Clulung) Bang, *Yü 19552* (A, E). TIBET: Tsarong, Salwin–Kui Chiang Divide, 28°75′N., *Forrest 19860* (A, E, K); Laktang, *Ward 3459* (E). **Burma:** flank of N'Mai-kha–Salwin Divide, 26°20′N., *Forrest 29654* (E); Adung Valley, 28°20′N., 97°45′E., *Ward 9572* (A).

3d. **Lyonia ovalifolia** (Wallich) Drude var. **ovalifolia**

Andromeda ovalifolia Wallich, Asiatic Res. **12:** 391. 1820. *Andromeda capricida* Ham. ex D. Don, *pro. syn.*, Prodr. Fl. Nepal. 149. 1825. *Pieris ovalifolia* (Wallich) D. Don, Edinb. New Philos. Jour. **17:** 159. 1834. *Xolisma ovalifolia* (Wallich) Rehder, Jour. Arnold Arb. **5:** 52. 1924. TYPE: Nepal, without definite locality, *Wallich s.n.*, May 1818 (holotype, BM?, not seen; presumed isotypes, A!, UC!).

Andromeda ovalifolia var. *cordata* Govan ex Wallich, Catal. Indian Pl. no. 763B. 1829. TYPE: [India, Uttar Pradesh], E. Saharanpur, *Wallich s.n.*, 16 April [?—nearly illegible] (lectotype, K-W (IDC 7394. 90: II. 4!)). This name was first published as either a species or a variety by Wallich (1820). Since a rank was not designated, the name was not validly published until 1829, when Wallich listed it as a variety of *Lyonia ovalifolia.*

Deciduous to semi-evergreen shrub to moderate-sized tree to 7.5(–18) meters tall. Buds 1–11.5 by 1–6.5 mm. Leaf blades ovate or elliptic to slightly obovate, (4–)6–15(–21) by (2–)3.5–8.5(–11.5) cm.; mesophyll unlignified; apex acuminate;

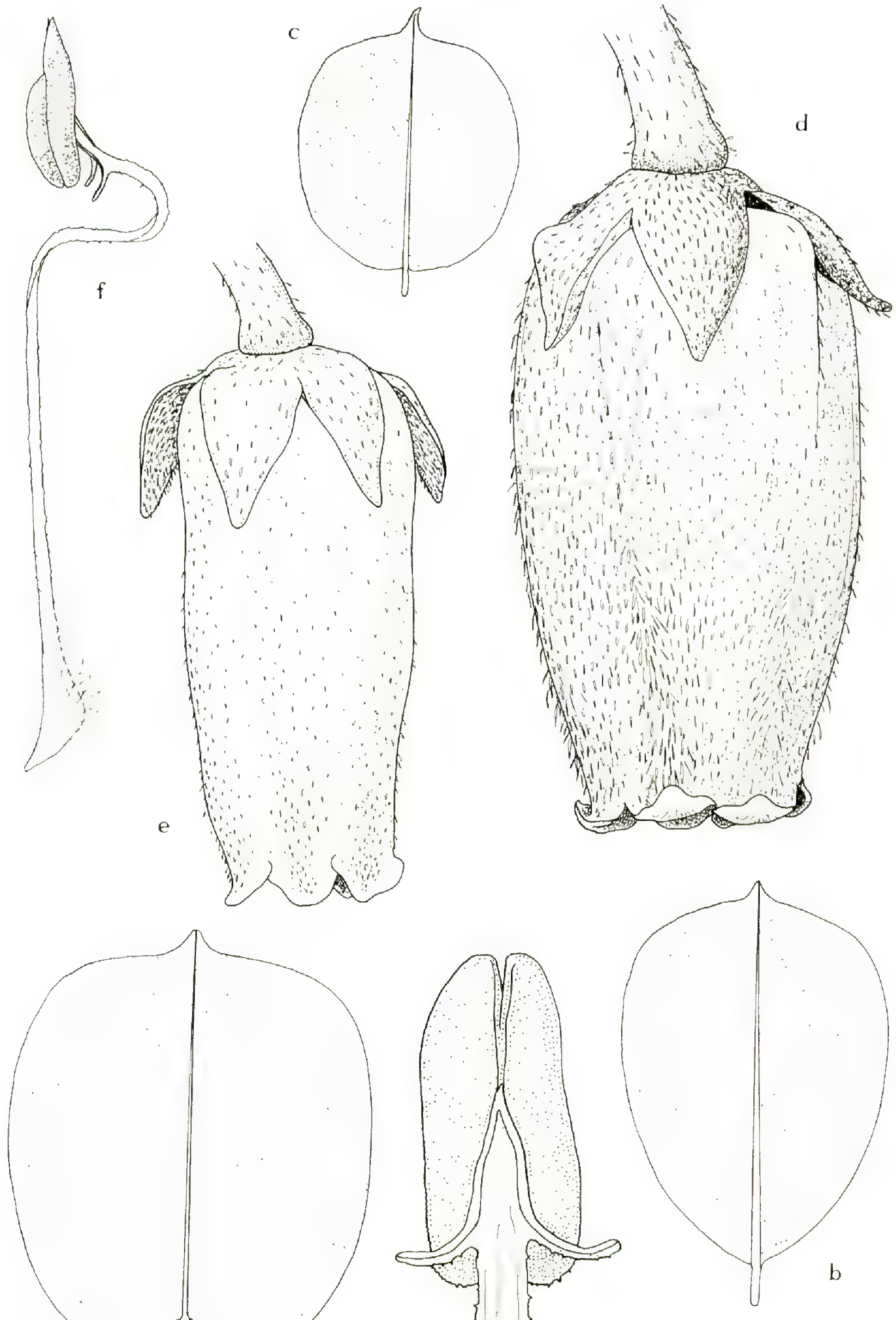


FIGURE 22. a–d, *Lyonia ovalifolia* var. *doyonensis:* a–c, leaves, × .5; d, flower, × 6. e–g, *L. ovalifolia* var. *ovalifolia* (in part): e, flower, characteristic of populations of western India, × 6; f, stamen, × 12.5; g, anther, × 25.

base rounded to cordate, or widely cuneate; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins usually smoothly arching toward margin; abaxial surface sometimes papillose and/or glaucous, usually not shiny yellowish- to gold-green, and glabrous or sparsely pubescent along proximal portion of midvein and occasionally also adjacent 2° veins; petiole 4–15(–20) mm. long. Inflorescences 3–16(–30) cm. long, usually with ca. 1 to 4 large, leaflike bracts to 2–8(–11.5) cm. long near base. Calyx lobes (1–)1.5–2.5(–4) by 0.8–1.5(–2) mm.; corolla cylindrical, (7–)8–12(–13.5) by 2.5–5(–7) mm.; filaments 5–9 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule usually subglobose to globose, 2.5–4.5 by 3.5–6 mm., with 5 pale, quite to sometimes only slightly thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURES 22, 23; see also Wallich (1820), Wight (1850), Sleumer (1967), Anonymous (1974a), and Hara (1968).)

DISTRIBUTION. China, western Kwangsi and Yunnan, south to Thailand and Malay Peninsula, west along Himalayas to northwestern India and Pakistan (MAP 6).

ECOLOGY. Cool- to warm-temperate areas; recorded from *Schima-Castanopsis* forests; various *Pinus* forests; rocky and rather dry slopes with oaks and/or pines; various *Quercus* forests; *Quercus-Vaccinium* thickets; *Quercus* spp.-*Keteleeria roulletii* forests, dry forests of *Quercus* spp. and *Rhododendron arboreum; Rhododendron* thickets; savannas with *Craibiodendron;* warm- to cool-temperate mixed broadleaved forests; dwarf, lichen-laden cloud forests; *Picea-Pinus* forests; *Tsuga dumosa* forests; *Abies spectabilis* forests (low portions); along streams, swamp, and forest margins; disturbed and/or burned areas; open sandstone savannas; ca. (700–)850–3050 m. alt. For more detailed discussions of the above-listed forest types, see Ohashi (1975), Stainton (1972), Malla *et al.* (1973), Suwal (1969), Schweinfurth (1957), and Hara (1966) for Nepal; Osmaston (1927), Parker (1924), Kanjilal *et al.* (1939) for India; Kingdon-Ward (1941, 1944, 1945) for Burma; Vidal (1960) for Laos; and Wang (1939) for Yunnan. Open, sunny areas favored; quite resistant to fires and often found in periodically burnt areas. Grows in cut-over and disturbed areas because of its sun-loving qualities and capability to spread vegetatively by underground rhizome network. Flowering chiefly (March to) April to July (to August), but varies greatly with elevation, latitude, and habitat.

COMMON NAMES. Muead-ngua (Thailand); nman-hpun (Jingpaw vern., northern Burma); anjīr, angiār (Brandis & Stewart, 1874), sagechu, sheabogi (Wallich, 1820), angri (Malla *et al.,* 1973) (Nepal); diengla samiang, jarahap (Khasi, Assam—Kanjilal *et al.,* 1939), ayār (Almora), aiaar, airee (Wallich, 1820), ailam (Kangra—Parker, 1924; Brandis, 1911), erau, yerta, yarta, ladrang, (Bashahr—Parker, 1924; Brandis, 1911), allain, ayatta, eilan, ellan, ellal, arur, rattankāt (Punjab—Brandis & Stewart, 1874; Brandis, 1911) (India); eyār, ayār (northwest frontier province, Brandis & Stewart, 1874), ratankáth (Hazara—Parker, 1924) (Pakistan).

REPRESENTATIVE SPECIMENS. **China.** KWANGSI: Bako Shan, W. Poseh, *Ching 7470* (A, E); Chen Pien distr., *Ko 55845* (A); Ling-yun Hsien, *Steward & Cheo*

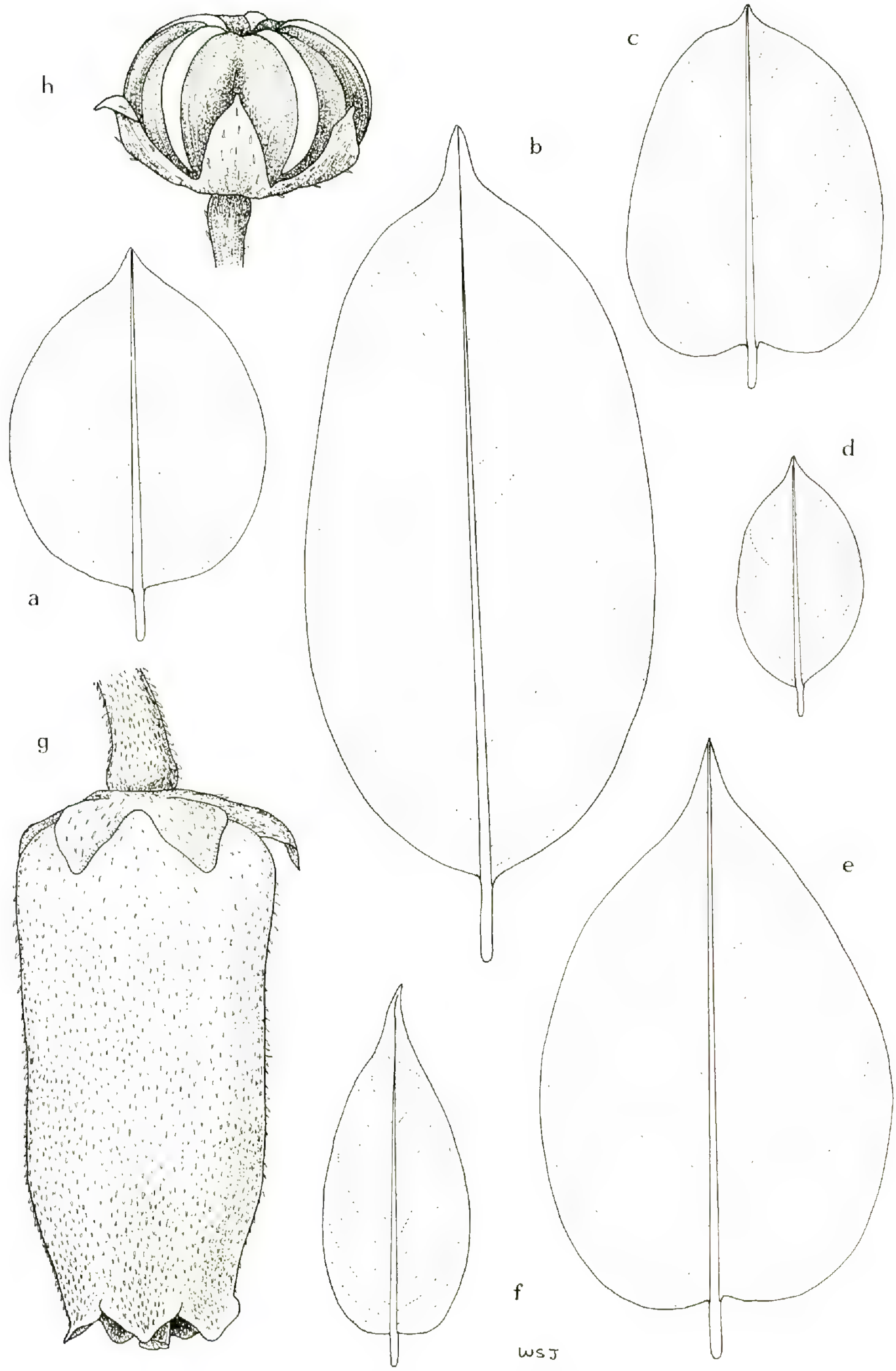


FIGURE 23. *Lyonia ovalifolia* var. *ovalifolia* (in part): a–f, leaves, × .5; g, flower, characteristic of Yunnan populations, × 6; h, capsule, × 6.

660 (A, S, W). YUNNAN: Yunnan-sen distr., *Cavalerie 4574* (E, K); Fo-Hai, *Fang 73855* (TAI); S. Chungtein, Ta-li, on Yangtze bank, *Fang 3212* (A); Wen-shan Hsien, *Fang 11065* (A); Mar-li-po, Chung-dzia, *Fang 12716* (A); Salween valley, near Lu-chang, 26°N., *Forrest 1107* (E); N'Maikha region, *Forrest 1820* (E); banks of Shweli, 25°N., *Forrest 7915* (E); W. flank of Shweli-Salween divide, 25°20′N., *Forrest 14633* (A, K, W); N'Maikha-Salwin divide, 26°20′N., *Forrest 18345* (A, E); vicinity of T'eng-yueh, 25°N., 98°36′E., *Forrest 24295* (E); W. of Lung-pan, 25°50′N., 98°33′E., *Forrest 27743* (A, E); Mengtse, *Henry 9091F* (A, E, S); between T'eng-yueh and Lung-ling, *Rock 7167* (A, UC, US); N. of Yunnan-fu, between Schi-lung-pa and Ta-sung-chu, *Schneider 374* (A); Shang-pa, *Tsai 54790* (A); Lung-ling Hsien, *Tsai 55015* (A); Ping-pien Hsien, *Tsai 60266* (A, E); W. of Champu-tung, Chiu-kiang, *Wang 67037* (A); Nan-chiao, *Wang 75258* (A); W. of Tung-hai, *Wissmann 44* (W); Shunning, Hila, Wumulung, *Yü 16655* (A, E); Kiukiang Valley, Lahpi to Tangtehwang, *Yü 19939* (A, E); Salween-Kiukiang divide, Swangchiang, *Yü 22086* (A, E). TIBET: Salween–Kui-chang divide, 28°40′N., 98°15′E., *Forrest 19136* (A, E, K); prov. Monyul, Nyam Jang Chu, Lepo, 27°47′N., 91°50′E., *Ludlow et al. 6453* (E); Shakti, Nyam Jang Chu, *Ludlow et al. 12566* (E); Tsangpo Gorge, *Ward 6373* (E, K); Tha Chu Valley, *Ward 19666* (E). **Vietnam:** Da-lat, *Hayata 593* (A); Valley of Dong-nai, *Poilane 9576* (P, US); E. of Dankia, Langbiang, *Poilane 18698* (P). **Laos:** Pu Bia, *Kerr 21045* (E); Sam Neua, *Poilane 2070* (A, B, K); Xing-huang, prov. Trammel, *Poilane 2258* (A, B); Pakson, Boloven plateau, *Poilane 28475* (L). **Cambodia:** M. de l'éléphant, *Poilane 264* (A, K). **Thailand:** S. side of Doi Suthep, Chiang Mai, 18°50′N., 97°54′E., *Abbe et al. 9286* (A, E, K, L); Phukrading, Loey, 16°55′N., 101°47′E., *Abbe et al. 9435* (A); Doi Pui, Chiang Mai, *van Beusekom & Phengkhlai 1270* (E, K, L); Phu Miang, Loey, *Hansen et al. 11147* (E, L); Doi Chong, 19°25′N., 98°18′E., *Hansen & Smitinand 12640* (E, L, P); Doi Angka, *Kerr 5321* (E); Me Tun, Chieng-mai, *Kerr 6241* (UC); Doi Chieng-dao, Payap, *Put 4492* (E). **Malaysia:** Perak, W. crest of Brinchang, 4°31′N., 101°17′E., *Abbe et al. 9754* (A, E, K, L); Kedah, Gunong Jerai, *Dolman KEP 20745* (K); Pahang, Gunong Baku Brinahang, *Henderson SFN 23594* (A); Pahang, Gunong Tahan, *Holttum SFN 31384* (A); Kedah, Kedah Peak, *Symington KFN 46848* (L); Cameron Highlands, Robinson Falls near Tanah Rata, *Sleumer 4662* (L). **Burma:** Mt. Victoria [Pakokku Hill Tracts], *Cooper 6006* (E, UC); Haka, *Dickason 7391* (A, E, L); Wunba Taung, Chin Hills, *Dickason 8461* (A, E, L); Lawksawk state, Ah Shai Myin, *Dickason 8716* (A, E, L); N'Maikha-Salween Divide, 26°00′N., *Forrest 29731* (E); Fort Stedman, *Huk s.n.*, Jan. 1893 (E, W); Kachin state, Sumprabum sub.-div., between Tsuptaung and Kanang, *Keenan et al. 3421* (A, E, K); Kanat Bum, *Keenan et al. 3455* (A, E, K); SE. Shan states, Keng Tung territory, Meh Lui valley, *Rock 2315* (A, UC, W); Kahao, Zayul R., *Ward 7154* (K); N. Triangle, Kachin state, *Ward 21200* (A, E). **Bhutan:** Chepcha Dimpu, *Cooper 1313* (E); Gichha Punakha, *Cooper 2761* (E); Tilagong Punakha, *Cooper 2821* (E); Samtengang, Tashi Choling, *Hara et al. 1118* (TI); Balfai, near Trashigong, *Ludlow & Sherriff 571* (E); Kyi La, Mangde Chu Valley, *Ludlow & Sherriff 3013* (E); Gyasa Dzong, Mo Chu, *Ludlow et al. 16526* (A, E); Tobran, Trashiyangse Chu, *Ludlow et al. 20490* (E). **Nepal:** Godawari, *Bhatt 330* (UC); above Dhunche, Gosainkund, *Hara et al. 69967* (TI); Dhankuta, *Hara et al. 6304475* (A, TI); Ghatte-khebang, *Hara et al. 6304482* (TI); Kakani, Kathmandu, *Kanai 674987* (TI); Trisuli Valley, Syabrubensi, *Lyon 31* (E); between Grang and Thare, E. side of Trisuli R., *Nicolson 2364* (US); Sindhu Palchok distr., below Helumbu, *Nicolson 2659* (US); Lekh Rangchi,

Polunin et al. 527 (E); Darma Tarke Khola, *Polunin et al. 4338* (A, E); Ranga Chauthaka, S. of Chakure Lekh, *Polunin et al. 5550* (A, E); Langtang Valley, *Schilling 497* (K); Arun Valley, Kandbari, E. of Dingla, *Stainton 102* (E); Tarakholagaon, W. of Beni, *Stainton et al. 165* (E); Arun Valley, Sedua, NW. of Num, *Stainton 677* (A, E); near Lumsum, *Stainton et al. 2566* (A, E); upper Buni Gandaki, 28°32′N., 84°90′E., *Stainton 3918* (E); Bhujung, NE. Chanpokhara, *Stainton et al. 5114* (E). **Bangladesh:** Chittagong div., *Cowan 1016* (E). **India.** ARUNACHAL PRADESH: W. corner of Apa tani Valley, Subansiri div., *Cox & Hutchinson 527* (E); Delei Valley, 28°20′N., 96°35′E., *Ward 8480* (K); Kahao, *Ward 19491* (E). NAGALAND: Naga Hills, Kohima, *Prain s.n.*, June 1886 (E, L, W). MANIPUR: Muku, *Watt 5074* (E); Metaiphum, *Watt 6075* (E); Khongui Valley, *Watt 6766* (E). MIZORAM: Lushai Hills, Chakang, *Parry 109* (L). MEGHALAYA: Mamlu, *Bar 20931* (L); near Upper Shillong, Khasia Hills, *Cox & Hutchinson 544* (E, K); Shillong Peak, *Rao 2766* (L); Khasia and Jaintia Hills, Umran, *Ruse 19* (A). SIKKIM: Pamianchi, Tingling Bridge, *Hara et al. 5319* (A, TI); Phalut–Dentam, *Hara et al. 5320* (A, TI); Lachen, *J. D. Hooker s.n.*, May 17 (K); Zenni Valley, *Smith & Cave 2718* (M, UC). WEST BENGAL: Darjeeling, *Lace 2300* (E); Darjeeling, Happy Valley, *Hara et al. 5322* (TI). UTTAR PRADESH: Naini Tal, Kumaon, *Brandis 1667* (M); Kumaon, forest near Shankola, *Duthie 3129* (K); Dehra Dun distr., vicinity of Musoorie, Woodstock, *Fleming 460* (A); Jehu Garhwal, *Gamble s.n.*, 1 April 1898 (K); Garhwal, Batanbasa, Adnalarange, *Inayal 25913* (K); Jaunsar, Kachanu, *Nand 171* (E); Siwalik and Jaunsar div., Chakrata, *Rai 30* (US); Garhwal, Gohrna-Ramni, *Rau 10111* (A). HIMACHAL PRADESH: Simla prov., Mahasu, *Brandis 1419* (A); Dalash-Chazahi, Kulu-Lahaul, *Drummond s.n.*, 19 May 1888 (E, K, UC); Simla, below Naldehoa, *Gamble 6018* (K); Kulu Valley, *Jain & Bharadwaja s.n.*, 13 June 1950 (A); Kangra, Baijnath, *Koelz 4538* (A, F, US); Kulu, Kakinal, *Koelz 8339* (A, UC); Chamba state, Bara, *Lace 735* (E); Bashahr state, Simla distr., Sarhan, *Parker 2984* (A); Chamba state, Almi, Belj Valley, *Parker s.n.*, 23 June 1919 (A); Kulu, Parhratti Valley, *Parkinson 3913* (E); Dharamsala, Kotwali Bazaar, *Stewart 1875* (A, S). **Pakistan:** Hazara distr., Siran Valley, *Ianyat 19902* (K); Azad Kashmir, Serimang, Punch, *Stewart & Nasir 25498* (F, GH, W).

3e. **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz. Symb. Sin. **7:** 788. 1936.

Andromeda lanceolata Wallich, Asiatic Res. **13:** 390. 1820. *Andromeda squamulosa* D. Don, Prodr. Fl. Nepal. 149. 1825. *Pieris lanceolata* (Wallich) D. Don, Edinb. New Philos. Jour. **17:** 159. 1834. *Pieris ovalifolia* (Wallich) D. Don. var. *lanceolata* (Wallich) Clarke in J. D. Hooker, Fl. Brit. India **3:** 461. 1882. *Xolisma ovalifolia* (Wallich) Rehder var. *lanceolata* (Wallich) Rehder, Jour. Arnold Arb. **5:** 52. 1924. TYPE: India, "in montosis Bengalae orientalis" [probably from Khasia Hills region] (not seen, but illustration in Wallich (1820) falls within variation pattern expressed by this taxon.)

Pieris kouyangensis Lévl. Bull. Acad. Int. Géogr. Bot. **12:** 253. 1903. TYPE: China, Kouy-Tchéou [prov. Kweichow], vicinity of Kouyyang [Kueiyang], sur les montagnes du Collège, 18 May 1898, *Bodinier 2264* (holotype, E!; fragment of holotype, A!; isotype, P!).

Pieris ulbrichii Lévl. Bull. Soc. Bot. France **53:** 205. 1906. TYPE: China, Kouy-Tchéou [prov. Kweichow], without definite locality, 15 May 1904,

Esquirol 42 (holotype, E!; fragment of holotype, A!; isotype, E!).

Vaccinium mairei Lévl. Bull. Acad. Int. Géogr. Bot. **25:** 21. 1915. TYPE: China, prov. Yunnan, brousse des montagnes à Kigo-Me-Ti, 3200 m. alt., May 1912, *E. E. Maire s.n.* (holotype, E!; isotype, A!).

Lyonia compta (Smith & Jeffrey) Hand.-Mazz. var. *stenantha* Hand.-Mazz. Symb. Sin. **7:** 790. 1936. TYPE: China, prov. Yunnan, near Yunnanfu [Kun-ming], S. of Djindien-se Temple, 2100 m. alt., 23 May 1917, *Handel-Mazzetti 13077* (holotype, W!; isotypes, A!, E!).

Pieris ovalifolia (Wallich) D. Don var. *tomentosa* W. P. Fang, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci. Sect. Bot. **10:** 241. 1938. TYPE: China, prov. Yunnan, Yung-jen-hsien, in ravines, 1700 m. alt., 24 May 1933, *Tsai 52887* (holotype, PE?, not seen; isotypes, A (2 sheets)!).

Deciduous to semi-evergreen shrub to small tree to 4(–10) meters tall. Buds 1–7.5 by 1–5.5 mm. Leaf blades elliptic or narrowly elliptic, to slightly ovate or obovate, 5–11(–14.5) by 2–4.8(–7) cm., mesophyll with at least partially developed layer of lignified cells near abaxial epidermis; apex acuminate; base narrowly cuneate to rounded; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins usually smoothly arching toward margin; abaxial surface neither papillose nor glaucous, often shiny yellowish- or gold-green, glabrous or sparsely pubescent along proximal portion of midvein to rarely densely pubescent on all veins; petiole 5.5–14 mm. long. Inflorescences 2.5–9(–18) cm. long; usually with 1 to 5 large, leaflike bracts to 2–7(–11) cm. long near base. Calyx lobes (2–)2.5–4.5(–6.5) by 0.8–1.7(–2.5) mm.; corolla cylindrical, (7–)8–10(–12.5) by 3–5.5(–6.5) mm.; filaments 5–7.5 mm. long, with spurs to ca. 0.5 mm. long. Capsule short-ovoid or ovoid, to less commonly globose or subglobose, 3–5(–5.5) by 3–4.5(–5) mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 24; see also Wallich (1820), Wight (1850), Anonymous (1974a).)

DISTRIBUTION AND ECOLOGY. China, Yunnan and southern Szechwan, eastward into Kweichow and Kwangsi; disjunct populations in Kwangtung and Hainan, China, and Khasia Hills, India (MAP 7). *Pinus* and/or *Quercus* forests, *Castanopsis* forests, thickets, open areas with *Pteridium*, open woods, dry, rocky hillsides and ridges, gulleys, forest margins; ca. (365–)1100–2800(–3050) m. alt. Flowering chiefly (March to) April to early June.

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG: P'oon-Ue distr., White Cloud Mt., *McClure Y-121* (A); near Canton, Pakwan, *Sampson 16440* (K). HAINAN: Ch'ang-Kiang distr., Ka Chik Shan, *Lau 1608* (A). HUPEH: En-shih Hsien, *Chow 1856* (A, E). KWEICHOW: Tsingchen, Gou-R-Tan, *Teng 90289* (A); Pa-na, Chengfeng, *Tsiang 4293* (E, S, UC); Sa-chui, Tungtze, *Tsiang 4813* (E, M); Fan-ching-shan, Yinkiang, *Tsiang 7773* (E); Tui-po, Pi-chieh, *Tsiang 8976* (A, E). KWANGSI: Pin-lam, *Ko 55574* (A); Luchen, Pei Loo, Min Shan, *Ching 5946* (W); Ling-Yun Hsien, *Steward & Cheo 300* (A, S); SE. of Shang-sze, Shap Man Taai Shan, near Ping Hoh Village, *Tsang 22148* (A, S); Kwei-lin distr., San-min village, P'an-ku-shan and Ch'ao-t'ien-shan, *Tsang 27984* (UC); Yao Shan, Ping Nan, *Wang 39323* (A). SZECHWAN: Chung Hsien, *Fang 446* (A); Nanchuan Hsien, *Fang 1087* (A, E, K); Omei, *Fang 3331* (A, E); near

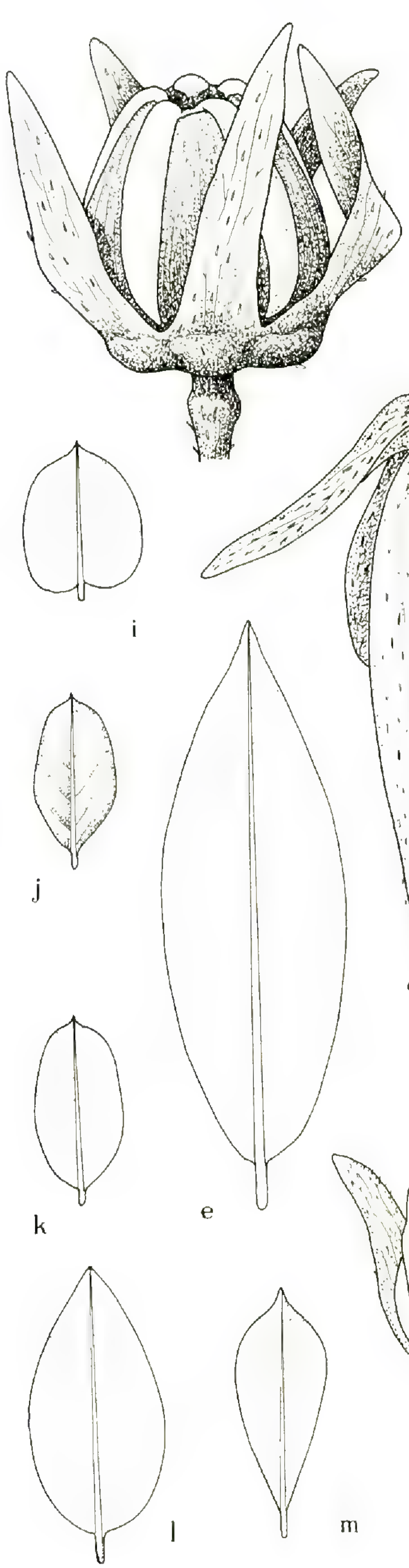
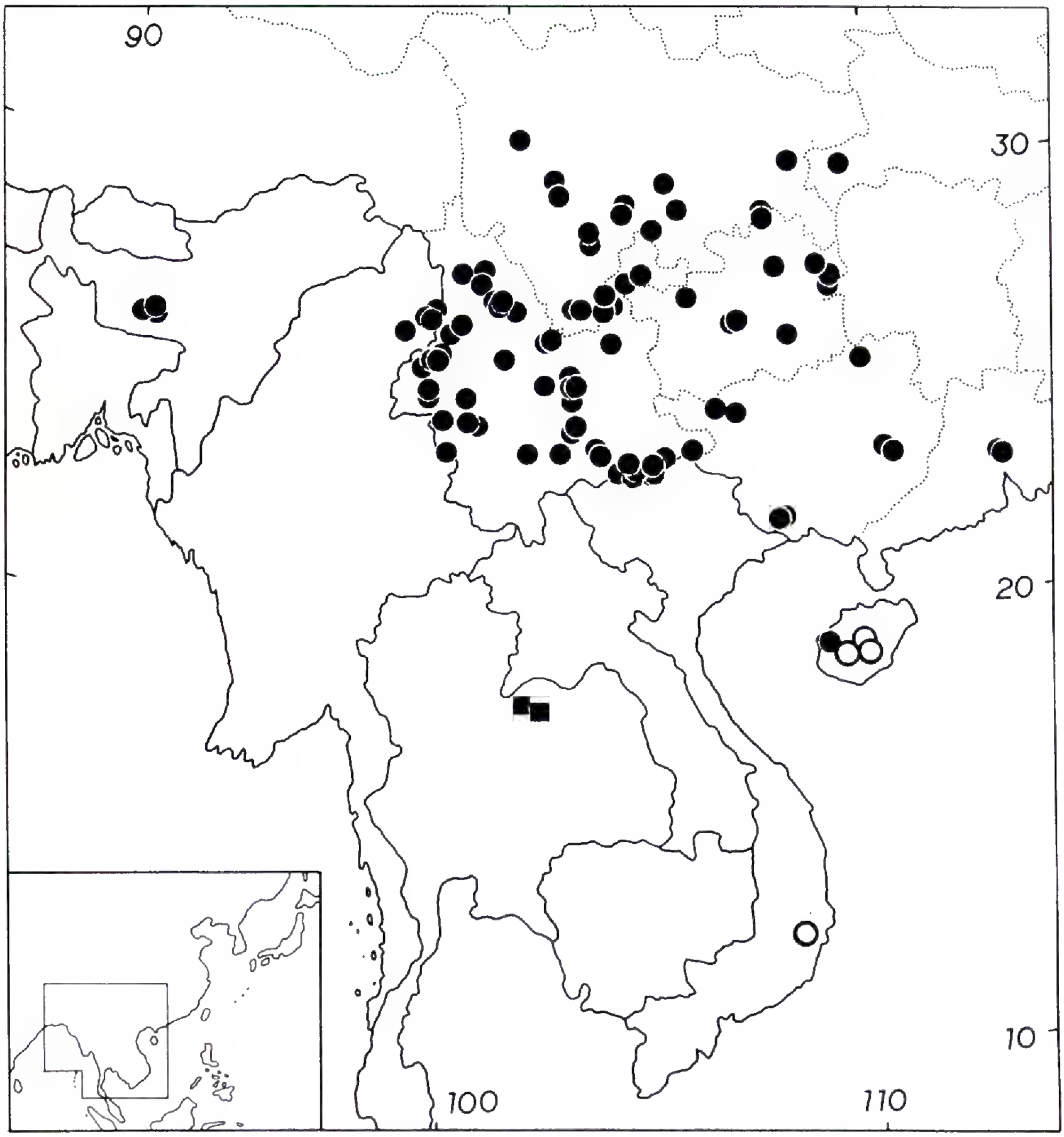


FIGURE 24. a–h, *Lyonia ovalifolia* var. *lanceolata:* a–e, leaves, × .5; f, flower, × 6; g, anther, × 25; h, capsule, × 6. i–n, *L. ovalifolia* var. *foliosa:* i–m, leaves, × .5; n, capsule, × 6.



MAP 7. Distribution of *Lyonia ovalifolia* var. *lanceolata* (dots), *L. ovalifolia* var. *rubrovenia* (circles), and *L. ovalifolia* var. *foliosa* (squares).

Ningyueh, *Handel-Mazzetti 1778* (E, W); Ya-lung valley, *Legendre 838* (P); Tachien-lu, *Wilson 1240a* (A, E, GH, K, W); Tung valley, *Wilson 3920* (A, K); O-pien Hsien, *Yü 746* (A); Juei-she Hsien, *Yü 973* (A); Huei-li Hsien, *Yü 1463* (A); Ping-shan Hsien, *Yü 5458* (E). YUNNAN: Yunnan-sen distr., Pin-fa, *Cavalerie 3887* (E, K); Likiang, Tze-li on Yangtze, *Ching 20261* (A); Chao-tung, *Ducloux 4942* (P); S. Chung-tien, Wu-tso on Yangtze bank, *Feng 3266* (A); Si-chour Hsien, Ting-mann, *Feng 12314* (A); Mar-li-po, Sze-tai-po, *Feng 13791* (A); W. of Yunnan-fu, 25°5′N., *Forrest 436* (E); flank of Gali Range, 25°40′N., *Forrest 4181* (E, K); near Teng-yueh, 25°N., *Forrest 7503* (A, E, K); Ghi-Shan, E. of Tali lake, 25°48′N., *Forrest 13472* (E, K); Shweli-Salwan divide, 25°6′N., 98°30′E., *Forrest 29566* (E); Dsolin-ho, *Handel-Mazzetti 6106* (M, W); Mengtsz, *Henry 9623A* (A, E); Feng Chen Lin, S. of Red R., *Henry 10510B* (E); near Yunnan-sen, *Maire 816/1914* (E); Tsu-yung, *McLaren's Collectors AA-130*

(E); Pa-pien Ho, between Mohei and Maokai, *Rock 2991* (A, UC, US); high plateau between Likiang and Tali-fu to foot of Likiang Snow Range, *Rock 3210* (A, US); Lotueshan, W. of Yangtze bend at Shiku, *Rock 8475* (A, UC, US); N. of Yunnan-fu, between Schi-lung-pa and Ta-sung-tchu, *Schneider 352* (A); between Poloti and Yungpeh, *Schneider 1690* (A, E, K); Yi-liang Hsien, *Tsai 52136* (A, E); Yung-jen Hsien, *Tsai 52794* (A); Kienshuei Hsien, *Tsai 53049* (A); Shih-ping Hsien, *Tsai 53352* (A, E in part); Ta-li Hsien, *Tsai 53876* (A, E in part); Shang-pa Hsien, *Tsai 54393* (A); Ping-pien Hsien, *Tsai 55075* (A, E); Lung-ling Hsien, *Tsai 55672* (A, E); Lan-ping Hsien, *Tsai 56216* (A); Tung-lung-tang, Cheng-kiang, *Tsaing & Wang 16312* (A); Wei-si Hsien, *Wang 64330* (A, TAI); Chen-kang Hsien, *Wang 72332* (A); Tsang-yuan, *Wang 73202* (A); Fo Hai, *Wang 73716* (A); Shunning, *Yü 16611* (A, E); Mienning, Poshang, *Yü 17896* (A, E); Mekong-Salwin divide, Alulaka, *Yü 19099* (A, E). **Burma:** Hpiman Hill, *R. F. & Cox 896* (E); Black Rock–Tang-tung rd., *Kermode 17246* (K); Htawgaw, Naung-chaung Valley, Lashi country, *Ward 1546* (E); Naung-chaung Valley, *Ward 1701* (E). **India.** MEGHALAYA: Khasia Hills, Shillong, *Burkill & Banerjee 50* (E); Khasia, *Herb. Griffith 3484/2* (GH, GOET, K, M, S, W), *J. D. Hooker & Thompson s.n.*, 2 Oct. 1850 (K); Khasya and Jaintia Hills, Nongstoin, *Panigrahi 16505* (L).

3f. **Lyonia ovalifolia** (Wallich) Drude var. **foliosa** (Fletcher) Judd, comb. et stat. nov.

Xolisma foliosa Fletcher, Kew Bull. **1936:** 40. 1936. *Lyonia foliosa* (Fletcher) Sleumer, Dansk Bot. Ark. **25:** 80. 1963. TYPE: Thailand, Loi, Kao Krading, ca. 1200 m. alt., 12 March 1924, *Kerr 8673* (holotype, E!; isotype, E!).

Deciduous to semi-evergreen shrub to 1–2(–4) meters tall. Buds 1–6 by 1–4 mm. Leaf blades elliptic to slightly ovate or obovate, 2.5–6(–7) by 1.4–3.3 cm.; mesophyll with 1 or 2 layers of lignified cells near abaxial epidermis; apex abruptly short-acuminate, to acute or rounded with small mucro; base narrowly cuneate to rounded or rarely cordate; venation eucamptodromous, 2° veins smoothly arching toward margin; abaxial surface neither papillose nor glaucous, light- or yellowish-green, glabrous; petiole 2–8 mm. Inflorescences (2–)3–7.5(–11) cm. long, usually with 3 to 9 rather large, leaflike bracts 0.8–4 cm. long near lower portion or scattered throughout. Calyx lobes 2.5–5(–6) by 0.8–1.5 mm.; corolla cylindrical, (6–)7–10(–11) by 3–5.5 mm.; filaments 5–6 mm. long, with 2 spurs to ca. 0.5 mm. long. Capsule short-ovoid or ovoid, 2.5–4 by 3–4.5 mm., with 5 pale, quite thickened sutures that in dehiscence remain attached to an adjacent valve. (FIGURE 24; see also Stevens, 1970, 1971.)

DISTRIBUTION AND ECOLOGY. Limited to sandstone plateau atop Poo Kradeng and near Wang-sa-phung in northern Thailand (MAP 7). Common in open savannas of *Pinus merkusii* and *P. insularis*, along with *Quercus*, many grasses, and sedges; ca. 1045–1300 m. alt. Flowering November through May.

REPRESENTATIVE SPECIMENS. **Thailand:** Prov. Loey, Phu Krading, *Abbe et al. 9400* (A, L), *Smitinand 309* (A), 16°52′N., 101°52′E., *van Beusekom et al. 4500* (K, L); Loei, Wang-sa-phung, *Dee 305* (L).

3g. **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd, Jour. Arnold Arb. **60:** 491. 1979.

Pieris rubrovenia Merr. Philip. Jour. Sci. **23:** 256. 1923. *Lyonia rubrovenia* (Merr.) Chun, Sunyatsenia **4:** 254. 1940. TYPE: China, summit of Five Finger Mt., ca. 1900 m. alt., 1 May 1922, *McClure, C.C.C. 9380* (holotype, PNH, not seen, photos at A, GH; isotypes, A (2 sheets)!, E!, NY (2 sheets)!, UC!, US!).

Pieris annamensis Dop in Lecomte, Fl. Gén. Indo-chine **3:** 726. 1930. *Lyonia annamensis* (Dop) Merr. Jour. Arnold Arb. **23:** 188. 1942. TYPE: Annam [Vietnam], Nha-trang, 1900 m. alt., 21 May 1922, *Poilane 3580* (holotype, P!; fragment of holotype, L!).

Pieris obliquinervis Merr. & Chun, Sunyatsenia **5:** 157. 1940. TYPE: China, [prov. Kwangtung], Hainan Is., Ting-On distr., Mo-Cheung, 30 Dec. 1933, *C. Wang 35986* (holotype, A!; isotypes, NY!, IBSC?, not seen).

Semi-evergreen shrub to ca. 5 meters tall. Buds 1–6 by 1–4.5 mm. Leaf blades obovate, ovate, elliptic, or narrowly elliptic (3–)4–9(–10) by 0.8–2.6(–3) cm.; mesophyll with 1 or 2 layers of lignified cells near abaxial epidermis; apex acuminate to acute (or obtuse); base narrowly cuneate to rounded; venation eucamptodromous to slightly brochidodromous toward apex, 2° veins smoothly arching toward margin; abaxial surface neither papillose nor glaucous, usually shiny yellowish to golden-green (occasionally reddish due to long-headed hairs), glabrous; petiole 6–11 mm. long. Inflorescences 2.5–7(–11) cm. long., with small bracts 2.5–7 mm. long throughout. Calyx lobes (2–)2.5–4 by 0.8–1.9 mm.; corolla cylindrical to elongate-urceolate, 5–7 by 3–3.5 mm.; filaments 3–4 mm. long, with 2 spurs to 0.2 or 0.3 mm. long. Capsule subglobose to globose, 2.5–4 by 3–4.5 mm., with 5 pale, slightly thickened sutures that in dehiscence remain attached to an adjacent valve or split irregularly. (FIGURE 25; see also Lecomte (1930), Anonymous (1974b).)

DISTRIBUTION AND ECOLOGY. Hainan and Vietnam (MAP 7). Woods, moist, dense forests, thickets, mountain ridges, often with pines; ca. 900–1900 m. alt. Flowering December and May.

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG. Hainan Is.: Fan Yah, Five Finger Mt., *Chun & Tso 44099* (A, B, PE, US); Bi-sha, *Hainan Expedition Team 759* (PE); Loktung, *Lau 27266* (A); without definite locality, *Wang 35569* (US). **Vietnam.** Nha-trang, *Poilane 3574* (A, B, P).

Lyonia ovalifolia is most closely related to *L. villosa*, which occurs chiefly at higher elevations (FIGURE 7). It differs from *L. villosa* in its larger and more commonly acuminate-tipped leaves, usually longer racemes, cylindrical flowers, and filaments with two spurs below the anther-filament junction.

Variation within Lyonia ovalifolia. Populations of *Lyonia ovalifolia* are separable into several morphologically distinct and geographically and/or ecologically isolated varieties. These varieties can be arranged into two groups based upon morphological and anatomical characters. *Lyonia ovalifolia* vars. *elliptica*, *hebecarpa*, and *doyonensis* are very similar and tend to have deciduous leaves with the secondary veins ± brochidodromous, sinuous or ± irregular,

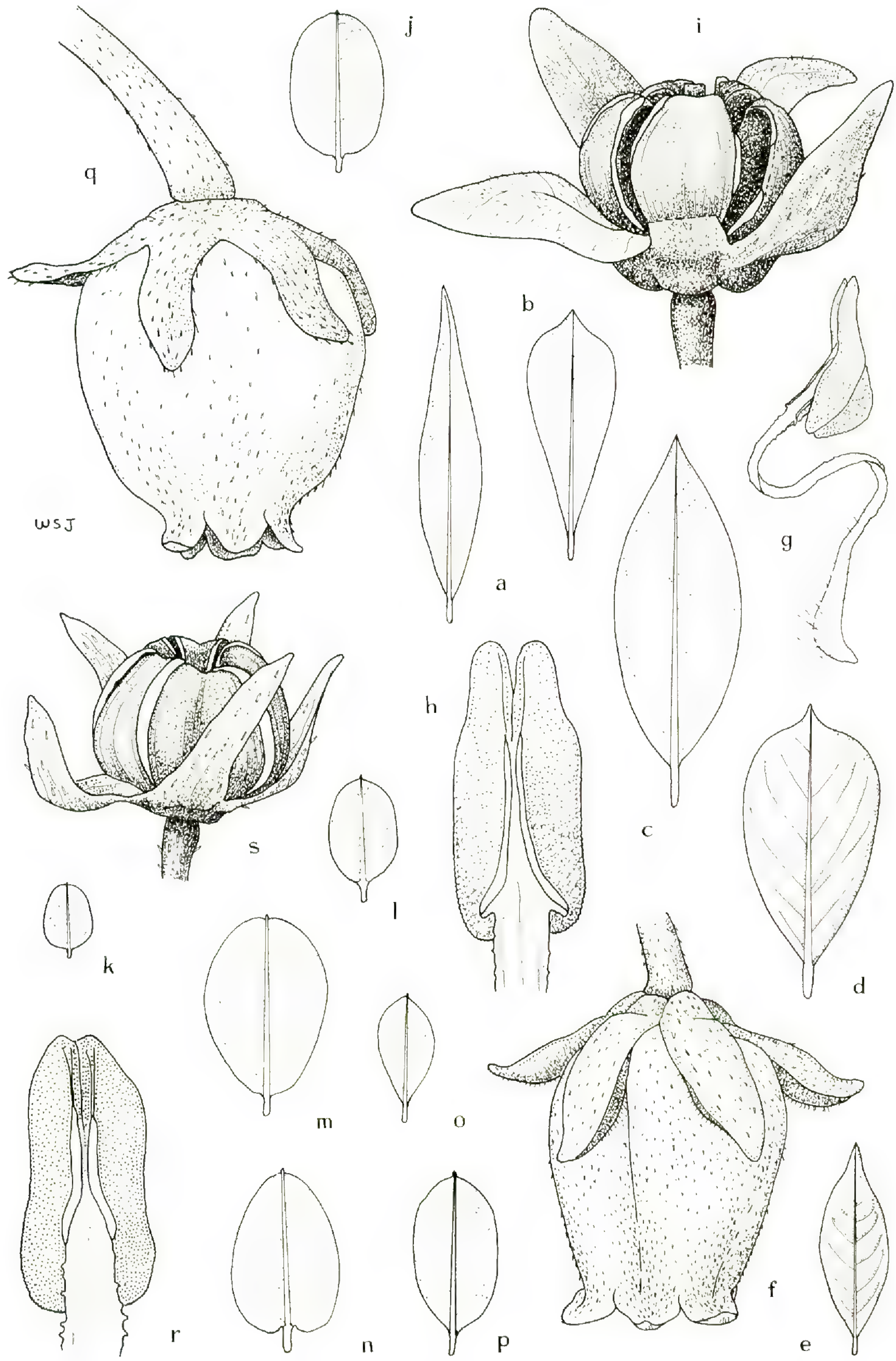


FIGURE 25. a–i, *Lyonia ovalifolia* var. *rubrovenia:* a–e, leaves, × .5; f, flower, × 6; g, stamen, × 12.5; h, anther, × 25; i, capsule, × 6. j–s, *L. villosa* var. *sphaerantha:* j–p, leaves, × .5; q, flower, × 6; r, anther, × 25; s, capsule, × 6.

and of varied strengths (i.e., intersecondary veins common) and angles of divergence from the midvein. The cells of the spongy mesophyll of the lamina are never lignified, and the calyx lobes tend to be very short. The capsules are globose to subglobose. In contrast, *L. ovalifolia* vars. *lanceolata, foliosa,* and *rubrovenia* have more coriaceous, deciduous to semi-evergreen leaves with the secondary veins ± eucamptodromous, ± uniform, and smoothly arching toward the margin. One or two layers of cells of the spongy mesophyll just above the abaxial epidermis are usually lignified, and the calyx lobes are usually elongated. The capsules are subglobose or globose to conspicuously and quite narrowly ovoid or short-ovoid. The abaxial leaf epidermis is usually a characteristic yellowish gold or yellowish green color upon drying. *Lyonia ovalifolia* var. *ovalifolia* fills the morphological gap between the two groups. It has deciduous to semi-evergreen leaves with the secondary veins usually smoothly arching toward the margin but with the mesophyll cells never lignified. Its calyx lobes are very small, except in populations from the western Himalayas, and its capsules are subglobose to globose.

There has been much confusion concerning the geographic range of *Lyonia ovalifolia* var. *elliptica,* from Japan and Taiwan, and the identity of plants referred to here as var. *hebecarpa,* which occurs in eastern China (see MAP 6). Nakai (1919) and Hara (1966) considered var. *elliptica* to be endemic to Japan, while Sargent (1913), Rehder (1924), Handel-Mazzetti (1936), and Ohwi (1965) thought that it also occurred in Taiwan and/or eastern China. Sargent (1913), Rehder (1924), and especially Hara (1966) very properly pointed out that var. *elliptica* (= subsp. *neziki*) differs from the related Himalayan and western Chinese plants (i.e., var. *ovalifolia,* as considered here) in its much thinner and smaller leaves with different secondary veins, its slightly smaller capsules and corollas, and its shorter racemes. But the situation was confused by these widely varying treatments of the plants of eastern China and Taiwan, and even Hara, who treated all related plants of the Himalayas, China, and Taiwan as *L. ovalifolia* subsp. *ovalifolia,* stated (1966, p. 648) that "some intermediate forms [i.e., between var. *elliptica* and var. *ovalifolia*] occur in China and Formosa." Although when compared to the Japanese plants, those of Taiwan tend to have slightly larger, less pubescent leaves, longer inflorescences and calyx lobes, and more often glabrous bud scales, the range of overlap in these characters is great, and the plants of the two islands cannot be consistently separated using these or any other morphological characters. Both also have the very characteristic ± dense tuft of long-unicellular hairs near the leaf base, which is not found in any other variety of *L. ovalifolia.* In contrast, the Taiwanese and Japanese populations are clearly distinguishable from those of such provinces as Chekiang, Fukien, and Kiangsi by the above-mentioned leaf pubescence pattern. In addition, they often have slightly smaller leaves, shorter racemes, and smaller flowers. The eastern Chinese plants are not only clearly different from the populations of Japan and Taiwan, but they are also distinguishable from the Himalayan plants, as previously mentioned. In fact, these differences were used by Sargent and Rehder in separating var. *ovalifolia* from their more inclusive var. *elliptica.* Thus, I consider *L. ovalifolia* var. *elliptica* to be endemic to Japan and Taiwan and refer the eastern China "intermediate

forms'' of Hara (1966) or the eastern China ''var. *elliptica*'' of Sargent (1913) or Rehder (1924) to the closely related var. *hebecarpa*.

Lyonia ovalifolia var. *hebecarpa* is essentially geographically isolated from both vars. *doyonensis* and *ovalifolia*, although the ranges of *hebecarpa* and *doyonensis* overlap slightly in northwestern Yunnan (compare MAPS 5 and 6), and *hebecarpa* and *ovalifolia* occur sympatrically in parts of Yunnan and western Kwangsi. In Yunnan altitudinal and ecological differences may also play a part in isolating these taxa: here var. *hebecarpa* occurs chiefly between ca. 2300 and 3300 meters, with var. *ovalifolia* from ca. 1100 to 3050 meters.

In northwestern Yunnan, where all three taxa occur together, specimens are often difficult to determine to variety, and hybridization probably takes place. Occasional puzzling and completely intermediate plants have been collected; for example, *Wang 64013* (Weisi Hsien, 3500 m.; A, TAI), *Henry 9091, 9091D* (Mengtze [Mengtzu]; A, E), and *Forrest 24356* (Shweli-Salwin divide, 8000–9000 ft.; E, K), all from Yunnan, are clearly intermediate between *Lyonia ovalifolia* vars. *hebecarpa*, *ovalifolia*, and/or *doyonensis*. In addition, there is a specimen (*R. A. 1658* (E!), probably from northern Burma) that is intermediate between vars. *ovalifolia* and *doyonensis* in leaf shape and venation characters. It is likely that all three taxa interbreed freely where they come into contact, and intermediate specimens seem to be completely fertile. It is often very difficult even to infer the exact parentage of these intermediate plants from herbarium specimens alone, and the situation needs to be thoroughly investigated in the field. A few specimens (placed here in var. *ovalifolia*) collected from high elevations in Sikkim and Nepal (e.g., *Smith & Cave 2718* (B, UC), and *Stainton, Sykes, & Williams 2870* (A, E)) also approach var. *doyonensis* in leaf shape and in prominence of secondary and tertiary veins.

Lyonia ovalifolia var. *hebecarpa* is quite variable in the shape and size of its leaves (see FIGURE 21); the amount and distribution of unicellular hairs on its leaves, capsules, and bud scales; the amount of glaucousness on the abaxial leaf surface; and the size of its flowers and fruits. The variability is greatest in Yunnan. As in var. *elliptica*, the leaves produced early in the growing season are frequently more strongly cordate than later-formed ones. In the fall the leaves often become reddish on the adaxial surface before dropping.

Lyonia ovalifolia var. *doyonensis* (a rare and local taxon) is in general aspect intermediate between vars. *hebecarpa* and *ovalifolia;* it is, however, immediately recognizable and differs from both in its large leaves with truncately short-acuminate apices, prominently abaxially raised secondary and tertiary veins, and length/width ratios of ca. 0.9–1.3(–1.5). In addition to the above characters, var. *doyonensis* differs from var. *hebecarpa* in its obscurely to clearly papillose abaxial leaf surfaces, and from var. *ovalifolia* in the often more irregular secondary veins.

Field work is necessary to determine the factors isolating *Lyonia ovalifolia* var. *doyonensis* from var. *ovalifolia*. Since in Yunnan var. *doyonensis* tends to occur above ca. 2500 meters and var. *ovalifolia* commonly grows down

to ca. 1200 meters, the two may be at least partially ecologically isolated.

As mentioned above, *Lyonia ovalifolia* var. *ovalifolia* is closely related to vars. *doyonensis* and *hebecarpa;* importantly, it also forms the connecting link between these varieties and var. *lanceolata.*

In Yunnan and adjacent areas *Lyonia ovalifolia* var. *ovalifolia* can be distinguished from var. *hebecarpa* by its differently shaped, more coriaceous, and often abaxially papillose leaves with more smoothly arching secondary veins, and from var. *doyonensis* by the length/width ratio of its leaves, by its more elongate and gradually acuminate leaf apices, and by its less prominently abaxially raised secondary and tertiary leaf veins.

This taxon is more variable than any other variety of *L. ovalifolia,* possibly because of the diversity of habitats in which it occurs and its very broad geographic range. Part of this variation is probably due to environmental or developmental factors; thus, plants in exposed and/or dry areas tend to have smaller leaves, and leaves produced early in the season tend to have more strongly cordate bases than those produced later. However, much is probably genetic (for example, variation in length of calyx lobes, appearance of the abaxial leaf epidermis, presence of papillae, and—to some extent—leaf shape) and correlates well with geography.

Lyonia ovalifolia var. *ovalifolia* is easily distinguished from var. *lanceolata* in Yunnan and adjacent regions, where the two occur sympatrically, by its often longer inflorescences, shorter calyx lobes, usually more globose or subglobose capsules, and more ovate and/or cordate leaves lacking a lignified layer of mesophyll cells just beneath the often glaucous and/or papillose abaxial epidermis. Plants of *L. ovalifolia* var. *ovalifolia* collected from northwestern India and some areas of Nepal, Bhutan, and Assam (especially at lower elevations) are much more similar to var. *lanceolata,* but even these plants can be distinguished (although sometimes only with difficulty) by their usually more globose or subglobose capsules, often slightly shorter calyx lobes, and more frequently cordate-based leaves that are slightly wider in relation to their width and that lack lignified mesophyll cells.

In northwestern India, Pakistan, Nepal, Bhutan, and Assam, there are plants that produce flowers with characteristically elongated calyx lobes ((1.5–)2–3(–4) mm.) and subglobose to globose capsules; the leaves are ovate to slightly cordate (less commonly, more or less elliptic), often dry a shiny bluish green color, and usually lack both papillae and a glaucous layer on the abaxial surface. These forms grade imperceptibly into plants with often larger, more consistently cordate to ovate, often abaxially glaucous and/or papillose leaves and slightly longer inflorescences as one moves to populations at increasingly higher elevations in the Himalayas. Papillose and/or glaucous specimens become common above ca. 2100 meters. As one travels eastward from Pakistan and northwestern India through Nepal, Bhutan, and Assam, into Burma, Thailand, Indochina, and Yunnan, the average length of the calyx lobes decreases from (1.5–)2–3(–4) mm. in northwestern India to only (1–)1.5–2(–2.5) mm. in Yunnan. In addition, the leaves become more frequently papillose and/or glaucous and more consistently cordate-ovate, and the inflorescences more elongated. Extreme forms characterized by very small

calyx lobes, long racemes, and often papillose and glaucous leaves occur in Yunnan and western Kwangsi, while plants from Thailand and Indochina sometimes have slightly irregular secondary veins toward the leaf apices. Thus, plants from the eastern portions of the range of var. *ovalifolia* (Yunnan, Kwangsi, Indochina, and Thailand) tend to resemble plants from the higher elevations in the Himalayas further west. It is thus much easier to differentiate vars. *ovalifolia* and *lanceolata* in Yunnan, where they come into contact, than it is to separate a specimen of var. *ovalifolia* collected in northwestern India from a specimen of var. *lanceolata* from Yunnan or Szechwan. *Lyonia ovalifolia* var. *ovalifolia* is probably chiefly geographically isolated from var. *lanceolata* although the factors isolating this taxon are in need of further investigation, especially since the varieties are more different morphologically when they occur sympatrically (in Yunnan) than they are when they occur separately!

The situation is complicated by the existence of a disjunct population of *Lyonia ovalifolia* var. *lanceolata* in the Khasia Hills of Assam (India). Many plants from this locality are indistinguishable from individuals of var. *lanceolata* collected from Yunnan, Szechwan, or Kweichow, yet they seem to intergrade completely with individuals of var. *ovalifolia,* which is the more characteristic variety of *L. ovalifolia* west of the Yunnan-Burma border (see *Griffiths 314* (GH, K, W); *Bot. Gard. Calcutta s.n.* (E, L); *Hooker & Thomson s.n.,* Nov. 1850 (E, K)). The explanation of this situation awaits further field studies.

In conclusion, it seems best (and most useful) to recognize *Lyonia ovalifolia* vars. *ovalifolia* and *lanceolata* as distinct taxa, in spite of their intergradation in the Khasia Hills, because 1) where they occur sympatrically in Yunnan, they are very different and do not seem to hybridize extensively; and 2) they have well-defined geographic ranges that overlap only slightly in Yunnan and Kwangsi, and within which they can usually be easily distinguished. In contrast, the high-elevation Himalayan and Yunnanese forms of *L. ovalifolia* var. *ovalifolia* have not been given formal taxonomic recognition as distinct from the low-elevation western Himalayan forms because these intergrade so completely across such an extensive geographic area that separating them would be completely arbitrary. They are thus maintained within a single variety, although it is recognized that the amount of morphological variation within this taxon is greater than that separating some other varieties of *L. ovalifolia,* such as vars. *lanceolata* and *foliosa,* or *hebecarpa* and *elliptica.* However, these varieties can be recognized since they are separated by a consistent and geographically correlated morphological gap.

Lyonia ovalifolia var. *lanceolata* is most closely related to vars. *rubrovenia, foliosa,* and *ovalifolia.* It can be differentiated from var. *rubrovenia* by its larger flowers; inflorescences usually with well-developed, leafy bracts; and capsules with more strongly thickened sutures. In addition, it tends to have less strongly lignified mesophyll cells. It can be distinguished from var. *foliosa* by its larger leaves with acuminate apices, inflorescences with leafy bracts usually limited to the base, and slightly larger capsules. Both of these varieties are geographically isolated from var. *lanceolata* (see MAP 7). *Lyonia ovalifolia* var. *lanceolata* is usually easily distinguished from var. *ovalifolia* by its

narrower leaves with cuneate to rounded bases and yellowish green abaxial surfaces, its often differently shaped capsules, its longer calyx lobes, and its shorter racemes.

Lyonia ovalifolia var. *lanceolata* is most variable in Yunnan, where forms with very large, very small, densely pubescent, or shortly and bluntly acuminate leaves occur. Some of this variation may be the result of crossing with other varieties of *L. ovalifolia*. A few specimens of var. *lanceolata* from Yunnan show some characteristics of var. *hebecarpa*, a taxon occurring at slightly higher elevations (ca. 2300–3300 vs. 1200–2800 m.) in this province, and *Maire 1068* (vicinity of Yun-nan-sen, Yunnan (E)), *Wang 65054* (Li-kiang Hsien, 2500 m., (A)), and *Tsai 57093* (NW. Yunnan (A, E)), probably represent hybrid individuals.

In *Lyonia ovalifolia* var. *lanceolata* there are sometimes branches with quite leafy-bracted racemes at nearly every node; herbarium material of such branches often lacks true leaves, although they appear leafy (see Wallich, 1820), since the plants are deciduous and flowering occurs on branches of the previous year. The bracts are usually narrower in relation to their length than are leaves from the same plant.

Lyonia ovalifolia vars. *foliosa* and *rubrovenia* are very closely related to var. *lanceolata*. Variety *foliosa* is distinctive due to its small leaves that have short petioles and abruptly short-acuminate to acute or rounded apices with a small mucro, and its inflorescences that often have conspicuous leaf-like bracts throughout. Variety *rubrovenia* is easily distinguished by its more consistently globose or subglobose capsules with the sutures less strongly thickened; its smaller corollas, filaments, and spurs; and its racemes that lack large, leaflike bracts.

Lyonia ovalifolia var. *rubrovenia* is quite variable in the size and the length/width ratio of its leaves. Forms that have larger and narrower leaves with more numerous veins have been described as *Pieris obliquinervis*, but there is complete intergradation between these plants and those with shorter and more abruptly acuminate leaves.

Nomenclature. The specimen at Leiden (Herb. no. 167) that Sleumer labeled as the type (i.e., lectotype) of *Andromeda elliptica* cannot have been a specimen on which the original description was based because it consists of two twigs in fruit and one with very young inflorescences—Siebold and Zuccarini (1846) described the twigs, leaves, inflorescences, and flowers, but not the fruits. Neither are two possible duplicates (also at L) likely to be type material: one (Herb. no. 168) is composed of one sterile twig, two twigs with mature capsules, and one small flowering scrap of a *Vaccinium;* the second (Herb. no. 169) includes one branch with mature capsules, and another with floral buds and newly opened flowers (nearly all with corollas smaller than the measurements given in the description). On all three sheets the most obvious feature of the plant is the presence of these characteristic subglobose capsules with pale, very thick sutures, and it is unlikely that Siebold and Zuccarini would have overlooked such a prominent part of the plant while describing the flowers in minute detail. The lectotype should probably be selected from

material sent to Siebold by H. Burger in 1842 (see earlier).

Pieris henryi Lévl. is probably best placed in synonymy under *Lyonia ovalifolia* var. *hebecarpa,* instead of under *Lyonia villosa* var. *pubescens* as was done by Rehder (1934). Its filaments have two spurs just below the junction with the anther, a condition not found in *L. villosa* but characteristic of *L. ovalifolia.* Also, its 2–2.5 mm. long calyx lobes would be anomalous in *L. villosa* var. *pubescens* (in which they are 2.5–5.5 mm. long), although they are within the normal range of variation of *L. ovalifolia.* Within *Lyonia ovalifolia,* its chartaceous, deciduous leaves, with their secondary veins ± irregular to sinuous and with a sparse covering of short, unicellular hairs abaxially along the midvein and many secondary veins, indicate an affinity with var. *hebecarpa.* According to a note on the type sheet (*A. Henry 9681*), J. Hutchinson also referred *Pieris henryi* to *L. ovalifolia.* This specimen is unusual because its mucronate-tipped leaves are only ca. 4 cm. long. Such small-leaved individuals (or populations?) also occur in several other varieties of *L. ovalifolia* in Yunnan.

Pieris ovalifolia var. *tomentosa* was described by Fang (1938) from a specimen on which nearly every part of the plant is more or less densely covered with unicellular hairs. The leaves have abruptly acuminate apices and smoothly arching secondary veins, the racemes are rather short (3–6.5 cm.), and the calyx lobes are only 2–2.5 mm. long. In Yunnan occasional specimens of *Lyonia ovalifolia* var. *lanceolata* (e.g., *Maire 1064*) have been collected that are nearly as pubescent, and the plant described by Fang is likely only an extremely pubescent form of this taxon.

Possible hybridization with other species. Lyonia villosa probably occasionally hybridizes with *L. ovalifolia* where they come into contact, and a specimen (*Rock 24400* (A, E, K, UC, US)) collected at 3800 meters in southwestern Szechwan (on Siga-shan) is morphologically intermediate. *Rock 24400* is probably a hybrid between *L. villosa* var. *pubescens* and *L. ovalifolia* var. *hebecarpa.* The differences between these two taxa and the characters of their putative hybrid are listed in TABLE 9. As can be seen, the specimen has the long calyx lobes and slightly smaller leaves of *L. villosa* and the spurs and long inflorescences of *L. ovalifolia.* Field studies are necessary to verify the identity of *Rock 24400* and to determine the causes and frequency of hybridization, as well as the isolating mechanism (probably ecological) operating.

Several collections of what may be hybrids between *Lyonia ovalifolia* (probably var. *ovalifolia*) and *L. villosa* (possibly var. *sphaerantha*) have been collected from rather high elevations in northern Burma and Yunnan (i.e., Burma, N. Triangle (Tama Bum), Kachin state, 9000–10,000 ft., *Ward 21101* (A, E); China, Yunnan, Salween-Kiukiang Divide, Wangtzang, 2600 m., *Yü 20214* (A, E); [Burma?], Chou-chi woods, 10,000 ft., *R. A. 1742* (E); [Burma?], Meku-ji Pass, 10,000 ft., *R. F. 1819* (E)). These plants are characterized by leaves that are strongly to only slightly cordate, 5–9.5 by 3–5.8 cm., with abruptly long-acuminate apices (the acumen often curved and/or folded over in pressing), and more or less brochidodromous and slightly irregular secondary veins. The abaxial surface is not papillose and

TABLE 9. **A comparison of Lyonia villosa var. pubescens, L. ovalifolia var. hebecarpa, and their probable hybrid.**

CHARACTER	*L. ovalifolia* var. *hebecarpa*	*Rock 24400* (probable hybrid)	*L. villosa* var. *pubescens*
LEAF LENGTH	5–12.5(–15) cm.	4.5–8 cm.	(2.5–)3–7(–8.5) cm.
LEAF APEX	Acuminate to long-acuminate	Slightly acuminate	Acute to rounded with mucro, or short-acuminate
ABAXIAL LEAF EPIDERMIS	Glaucous or not	Glaucous	Usually glaucous
2 SPURS NEAR APEX OF FILAMENT	Present	Present	Lacking
RACEME LENGTH	(2.5–)3.5–12(–16) cm.	4.5–11 cm.	1–4(–6) cm.
CALYX LOBE LENGTH	1–2.5(–3) mm.	2.5–3.5 mm.	(2–)3–5(–6.5) mm.
ELEVATION	Ca. 900–3300 (–3800) m.	Ca. 3800 m.	Ca. (1800–)2300–3800(–4100) m.

usually has rust-colored veins due to a dense covering of ferrugineous, multicellular, long-headed hairs. The racemes are usually 4–9.5 cm. long and have several large, leaflike bracts near the base. The corollas are 5–7.5 mm. long, the calyx lobes are 1.5–2.5 mm. long, and the filaments are without spurs. The capsules are subglobose to globose, to ca. 3 by 4 mm., with only slightly thickened sutures. Although it is difficult to determine the origin of these plants without field and crossing studies, they are probably hybrids between *L. ovalifolia* and *L. villosa* since they have the unappendaged filaments and more or less irregular secondary veins of *L. villosa,* along with the large, acuminate-tipped leaves and elongated, leafy inflorescences of *L. ovalifolia.* In addition, they have only been collected in regions (and at elevations) where both taxa can be expected to occur.

4. **Lyonia villosa** (Wallich ex Clark) Hand.-Mazz. Symb. Sin. **7:** 789. 1936.

Deciduous low shrub to small tree to 3.5(–9) meters tall with brownish to gray, longitudinally furrowed bark, sometimes spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly ridged, slender to less commonly stout, sometimes with few long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1–13 by 1–4 mm., often reddish. Leaf blades elliptic to slightly ovate, obovate, or nearly orbicular, (1.8–)2.5–8.5(–10) by (1–)1.5–5(–5.5) cm., ± flat, ± chartaceous to slightly coriaceous, ca. 0.1–0.3 mm. thick, often turning reddish in autumn; apex acute, obtuse to rounded with short to elongated (to ca. 4 mm.) mucro, or short-acuminate; base usually broadly cuneate to slightly cordate; margin

entire, plane to slightly revolute; venation brochidodromous (to slightly eucamptodromous near base), with 3° veins percurrent to reticulate; adaxial surface with sparse long-headed hairs, otherwise often glabrescent, sparsely to densely pubescent on midvein, sometimes extending to 2° veins, the 3° and higher order veins obscure to slightly visible, the 2° veins sometimes slightly depressed; abaxial surface strongly to obscurely papillose or ± smooth, usually glaucous, with sparse long-headed hairs, otherwise glabrous to densely pubescent along midvein, sometimes extending to many 2° (and occasionally even 3°) veins, the 3° and higher order veins obscure to slightly visible, the 2° veins slightly raised and visible, ± sinuous or irregular; petiole 2–13 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually below vegetative buds; inflorescences racemose, to 6- to 12- (to 18-)flowered, (0.5–)1–4(–7) cm. long, horizontal to slightly ascending; flowers pendulous and secund. Pedicels usually slender, 2.5–8.5(–10) mm. long, with long-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, narrowly triangular to linear, 1–5 mm. long; bracts extremely variable, usually 1 to 4 large and leaflike near base of raceme or scattered throughout (but inflorescence often appearing leafy throughout due to its shortness), the others small, similar to bracteoles in shape, usually caducous. Flowers 5-merous; calyx lobes narrowly triangular to linear, with slightly acuminate, acute to rounded apices, (2–)3–5(–6.5) by 0.5–1.8(–2) mm., the adaxial side often with few long-headed hairs, otherwise glabrous to densely pubescent, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent; corolla cylindrical to urceolate, 4.5–9(–11) by 3–7.5(–8) mm., white and sometimes slightly pink tinged, abaxially with sparse to moderate long-headed hairs; filaments with long-unicellular hairs, especially near base, 3.5–6 mm. long, unappendaged, anthers 1.1–1.6 mm. long; ovary glabrous to sparsely or less commonly moderately pubescent, placentae subapical to central. Capsule ovoid to short-ovoid to globose or subglobose, sometimes with apex slightly constricted, 2.5–4(–4.5) by 3–4.7(–6) mm., usually lacking long-headed hairs, otherwise glabrous to sparsely pubescent, with pale, thickened sutures that in dehiscence usually remain attached to an adjacent valve; seeds 0.7–1.1 mm. long.

DISTRIBUTION. In an arc from southwestern Szechwan and northern Yunnan (China), westward to Nepal and northwestern India; various habitats, ca. (1800–)2300–3800(–4100) m. alt.

Key to the Varieties of *Lyonia villosa*

1. Pedicels usually glabrous or with few short, curled hairs toward base; corollas urceolate, 4.5–6.5(–7) mm. long; leaves usually 2–4.5 cm. long, abaxial surface strikingly papillose, with midvein and secondary veins glabrous; [chiefly Yunnan, northern Burma, and southeastern Tibet] . . . . . 4b. var. *sphaerantha*.

1. Pedicels very slightly to densely pubescent; corollas urceolate to cylindrical, 4.5–9(–11) mm. long; leaves (3–)3.5–8.5(–10) cm. long, abaxial surface at most slightly papillose, with veins pubescent or not.
   2. Corollas urceolate, 5.5–8 by 4.5–7.5(–8) mm.; abaxial leaf surface usually

± papillose, glabrous on veins; pedicels very sparsely to moderately covered with short, usually much-curved, unicellular hairs; capsules subglobose to short-ovoid, apex not constricted; [Bhutan, Sikkim, Nepal, and northern India] . . . . . 4a. var. *villosa*.

2. Corollas cylindrical to occasionally urceolate, (4.5–)6.5–9(–11) by 3–4.5(–6) mm.; abaxial leaf surface often epapillate, occasionally obscurely papillose, often pubescent on midvein or secondary veins; pedicels moderately to densely covered with long, erect to curled, unicellular hairs; capsules ovoid to subglobose, apex often slightly constricted; [southeastern Tibet, Szechwan, and northern Yunnan] . . . . . 4c. var. *pubescens*.

4a. **Lyonia villosa** (Wallich ex Clark) Hand.-Mazz. var. **villosa**

Pieris villosa Wallich ex Clark in J. D. Hooker, Fl. Brit. India **3:** 461. 1882. *Andromeda villosa* Wallich, Catal. Indian Pl. 762. 1829, *nomen nudum*. *Xolisma villosa* (Wallich ex Clark) Rehder, Jour. Arnold Arb. **5:** 1924. TYPE: Nepal, Andromeda 762, Aug. 1821, *N. Wallich s.n.* (lectotype, K-W (IDC 7394. 90: I. 8!)).

Deciduous shrub to small tree to 3.5(–9) meters tall. Twigs glabrous to very sparsely pubescent. Buds glabrous. Leaf blades (3.5–)4–8(–10) by (2–)3–5.3 cm.; apex acute to rounded with short (to ca. 4 mm.) mucro; abaxial surface usually papillose or obscurely so (occasionally lacking papillae) and glabrous; petiole 5–13 mm. long, adaxially pubescent. Inflorescences 1.5–4(–7) cm. long. Pedicels very sparsely to moderately and usually short-crisped-pubescent. Calyx lobes (3–)3.5–5(–6) mm. long, abaxial surface usually glabrous; corolla urceolate, 5.5–8 by 4.5–7.5(–8) mm.; ovary glabrous. Capsule subglobose to short-ovoid, 3–4(–4.5) mm. long, glabrous. (FIGURE 26.)

DISTRIBUTION AND ECOLOGY. Nepal to Bhutan and adjacent areas of northern India and Tibet (MAP 8). *Rhododendron* forests and thickets, mixed temperate forests, *Betula utilis* forests, *Pinus* and/or *Quercus* forests, mixed forests in which *Pinus excelsa* is locally dominant, open woods and ridges (see Stainton, 1972); ca. (2150–)2750–3800(–3950) m. alt. Flowering chiefly May through July, probably peaking in June.

REPRESENTATIVE SPECIMENS. **China.** TIBET: Yatung, 27°51′N., 88°35′E., *Hobson s.n.*, 1897 (K). **Bhutan:** Tashing, *Cooper 1515* (E); Phajudin Thimphu, *Cooper 2543* (E); Paro, *Cooper 3568* (E); Dumthang, Ha Valley, *Ludlow & Sherriff 46* (E); Bela La near Pan, *Ludlow & Sherriff 163* (E). **Nepal:** Dor–Tinjure–Tinjure Phedi–Chauke, *Kanai et al. 726636* (TI); Suke–Kokim Pokhari–Hati Surde–Hile Chok, *Kanai et al. 726637* (TI); Khumbu, Khumzung, *Poelt s.n.*, 5 Oct. 1962 (M); Langtang Valley, *Polunin 539* (E); Khaptar forest, *Ram 511* (A); Thogundanda-Kaligad, *Shrestha 4188* (US); Lete, S. of Tukucha, Kali Gandaki, *Stainton et al. 974* (E); Sauwala Khola, *Stainton et al. 3020* (E); Bhurungdi Khola, *Stainton et al. 5808* (E); Rambrong, Lamjung Himal, *Stainton et al. 6048* (A, E); Siringdham, 22°20′N., 87°57′E., *Williams 605* (M). **India.** SIKKIM: Tonglu, *Hara et al. 69733* (TI); Lachen, *J. D. Hooker s.n.*, 29 May 1849 (K). WEST BENGAL; Darjeeling, Palmajua, *Cowan s.n.*, 4 June 1916 (E). UTTAR PRADESH: E. Almora division, Gon Valley, *Osmaston 1509* (A); Kumaon, Rur Gap, *Strachey & Winterbottom 2* (GH).

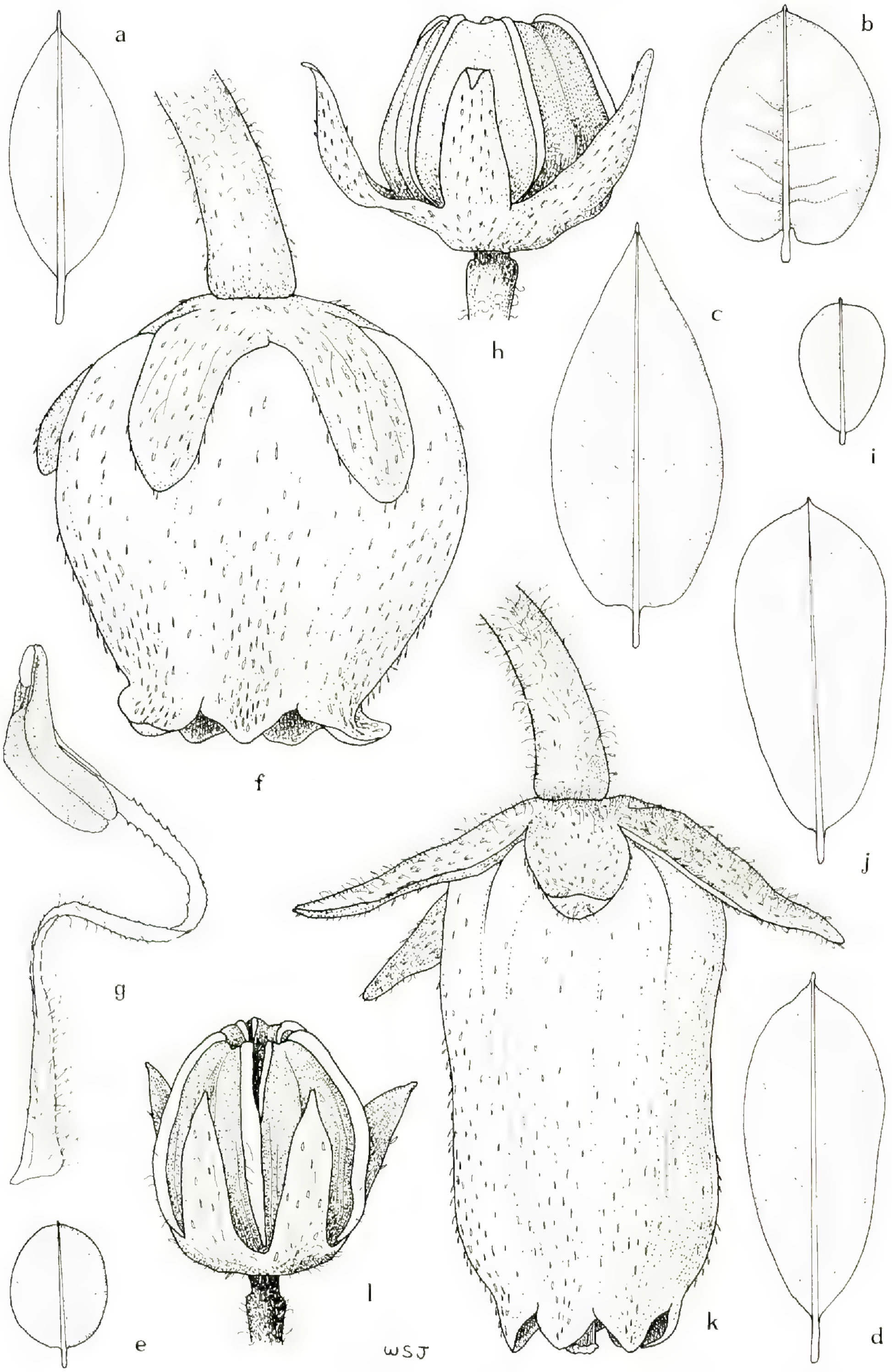
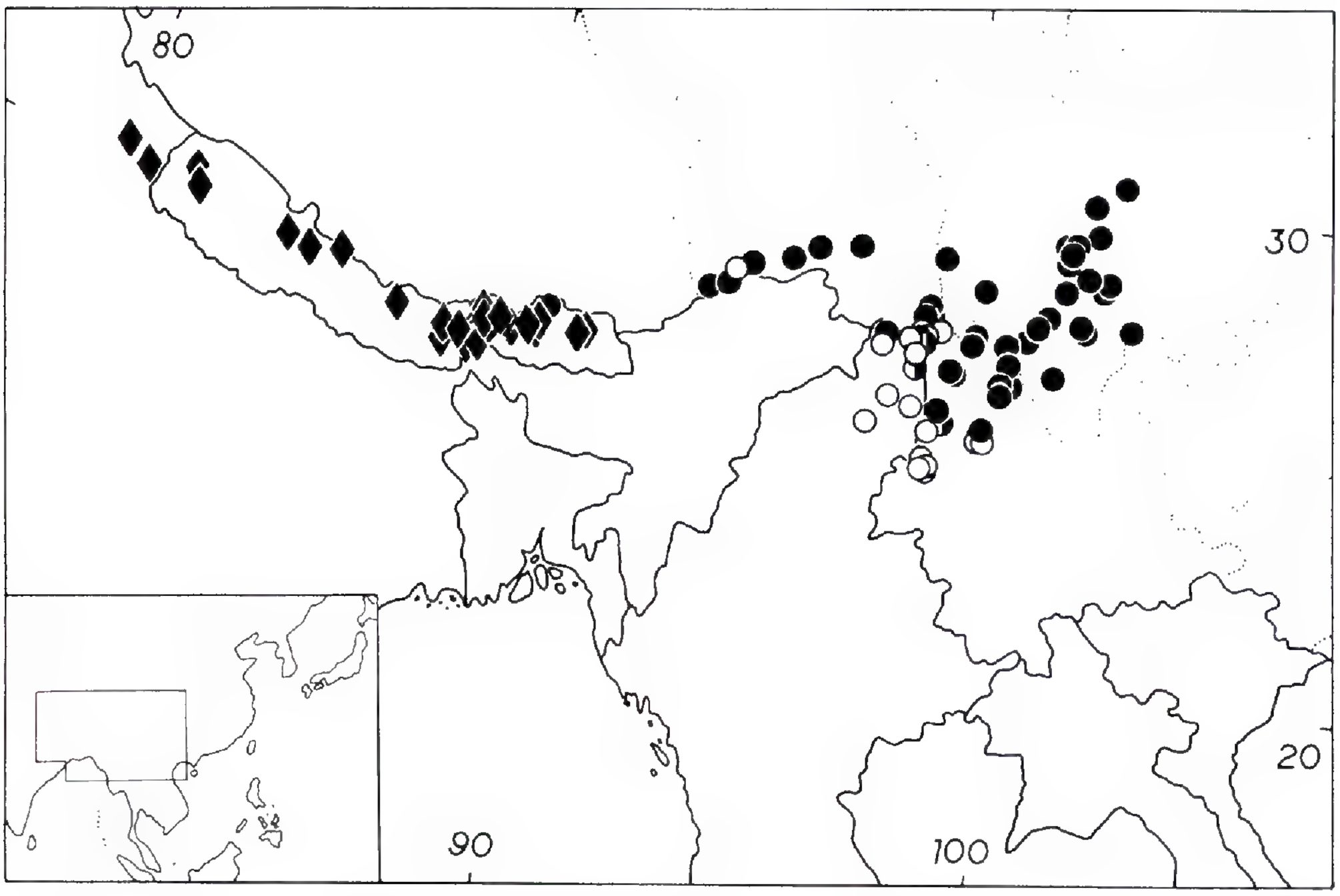


FIGURE 26. a–h, *Lyonia villosa* var. *villosa:* a–e, leaves, × .5; f, flower, × 6; g, stamen, × 12.5; h, capsule, × 6. i–l, *L. villosa* var. *pubescens* (in part): i, j, leaves, × .5; k, flower, × 6; l, capsule, × 6.



MAP 8. Distribution of *Lyonia villosa* var. *villosa* (diamonds), *L. villosa* var. *sphaerantha* (circles), *L. villosa* var. *pubescens* (dots), and intermediates between vars. *sphaerantha* and *pubescens* (half-blackened circles).

4b. **Lyonia villosa** (Wallich ex Clark) Hand.-Mazz. var. **sphaerantha** (Hand.-Mazz.) Hand.-Mazz. Symb. Sin. **7:** 789. 1936.

Xolisma sphaerantha Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. **62:** 131. 1925. TYPE: China, prov. Yunnan, between Mekong and Salween rivers, ca. 3200–3500 m., 16 June 1916, *Handel-Mazzetti 8918* (holotype, w!; isotypes, A!, E!).

Deciduous low to erect shrub or rarely small tree to 2.5(–4.5) meters tall. Twigs glabrous to very sparsely pubescent. Buds glabrous. Leaf blades (1.8–)2.5–4.5(–6) by (1–)1.5–3.5 cm.; apex usually obtuse to rounded with short (to ca. 2.5 mm.) mucro; abaxial surface strikingly papillose and glabrous; petiole 2–6 mm. long, adaxially pubescent. Inflorescences (0.5–)1–2.5(–3) cm. long. Pedicels glabrous or very sparsely crisped-pubescent near base. Calyx lobes (2.5–)3–4.5(–5) mm. long, abaxial surface glabrous; corolla urceolate, 4.5–6.5(–7) by 3.5–5.5(–6) mm.; ovary glabrous. Capsule subglobose to short-ovoid, 2.5–3.5(–4) mm. long, glabrous. (FIGURE 25.)

DISTRIBUTION AND ECOLOGY. Northern Burma, northwestern Yunnan, and southeastern Tibet (MAP 8). Mixed cool-temperate forests, *Pinus* or *Abies* forests, *Rhododendron* forests or thickets, rocky meadows and shrub-covered slopes and ridges; (2000–)2750–3600(–3800) m. alt. Flowering May through August, probably peaking June and July.

REPRESENTATIVE SPECIMENS. **China.** YUNNAN: Yangtze-Mekong divide, Lopa and Shupa valleys, 28°N., *Forrest 435* (E); E. flank of Tali Range, 25°40′N., *Forrest 4184* (E); Mekong-Salwin divide, 28°12′N., *Forrest 14986* (E, K); Shweli-Salwin divide, 25°30′N., 98°58′E., *Forrest 24265* (E, NY, US, W); N' Maikha-Salwin divide, 26°20′N., *Forrest 17999* (A, E, K); Ta-li, Mt. Tsang-chan, *Delavay 1889* (A, F, P); Ta-li Hsien, *Wang 63203* (A); Champutung, Shi-gi-tung, *Wang 67121* (A); Salwin-Kiukiang divide, Newahlung, *Yü 19302* (A); Taron-Taru divide, Bucalwang Valley, *Yü 20085* (A, E). TIBET: Kongbo prov., Tum La, Nayu, 29°N., 94°E., *Ludlow et al. 5804* (A, E). **Burma:** Hpiman Pass, *R. A. 1069* (E); Shing-Hong Camp, *R. A. 1642* (E); N'mai-Kha-Salwin divide, 26°25′N., *Forrest 29656* (E); Kachin state, Sumprabum subdiv., E. approaches from Sumprabum to Kumon Range, Bumpha Bum, 26°40′N., 97°20′E., *Keenan et al. 3538* (A, E); frontier of Tibet and Burma, Senighku Wang (Advance Base), *Ward 6890* (K); Adung Valley 28°20′N., 97°45′E., *Ward 9749* (A, in part); N. Triangle (Tama Bum), Kachin state, *Ward 20998* (A, E).

4c. **Lyonia villosa** (Wallich ex Clark) Hand.-Mazz. var. **pubescens** (Franchet) Judd, comb. nov.

Pieris ovalifolia (Wallich) Drude var. *pubescens* Franchet, Nouv. Arch. Mus. Paris, sér. 2. **10:** 44. 1887. *Pieris villosa* Wallich ex Clark var. *pubescens* (Franchet) Rehder & Wilson in Sarg. Pl. Wilsonianae **1:** 554. 1913. *Xolisma villosa* (Wallich ex Clark) Rehder var. *pubescens* (Franchet) Rehder, Jour. Arnold Arb. **5:** 53. 1924. TYPE: China, prov. Tibet oriental [actually Szechwan], Moupine [Poshin], "in regione maxime excelsa," Aug. 1869, *David s.n.* (not seen).

Deciduous low to erect shrub to 3.4(–4.5) meters tall. Twigs sparsely to densely pubescent. Buds glabrous to densely pubescent. Leaf blades (2.5–) 3–7(–8.5) by (1–)1.5–4(–5.5) cm.; apex acute to rounded with short (to ca. 4 mm.) mucro, or shortly acuminate; abaxial surface often smooth, at most obscurely papillose, very sparsely to densely pubescent along midvein (especially proximal portion) and often along many 2° (and occasionally even 3°) veins, or occasionally completely glabrous; petiole (2.5–)3–10 mm. long, pubescent adaxially or all around. Inflorescences 1–4(–6) cm. long. Pedicels moderately to densely crisped- or straight-pubescent. Calyx lobes (2–)3–5(–6.5) mm. long, abaxial surface glabrous to sparsely or densely pubescent; corolla cylindrical to less commonly urceolate, (4.5–)6.5–9(–11) by 3–4.5(–6) mm.; ovary glabrous to moderately pubescent. Capsule ovoid to globose, (2.5–)3–4.5 mm. long, glabrous to sparsely pubescent. (FIGURES 26, 27; see also Anonymous, 1974a.)

DISTRIBUTION AND ECOLOGY. Southeastern Tibet, extreme northern Burma, northern Yunnan, and southwestern Szechwan, with disjunct occurrence in Bhutan (MAP 8). *Pinus* forests, *Quercus-Ilex* forests, bamboo thickets, *Larix* and *Abies* forests, rocky openings in *Rhododendron* thickets, mixed temperate forests, dense thickets, forest margins, and rocky, scrub-clad slopes; (1800–) 2300–3800(–4100) m. alt. Flowering mainly late May through July.

REPRESENTATIVE SPECIMENS. **China.** SZECHWAN: Ta Hsieng Ling, Han Yueh, *Chiao 1615* (A); Pao-hsing Hsien, *Chu 3416* (A, E, K); Daliang-schan, E. of Ningyueh,

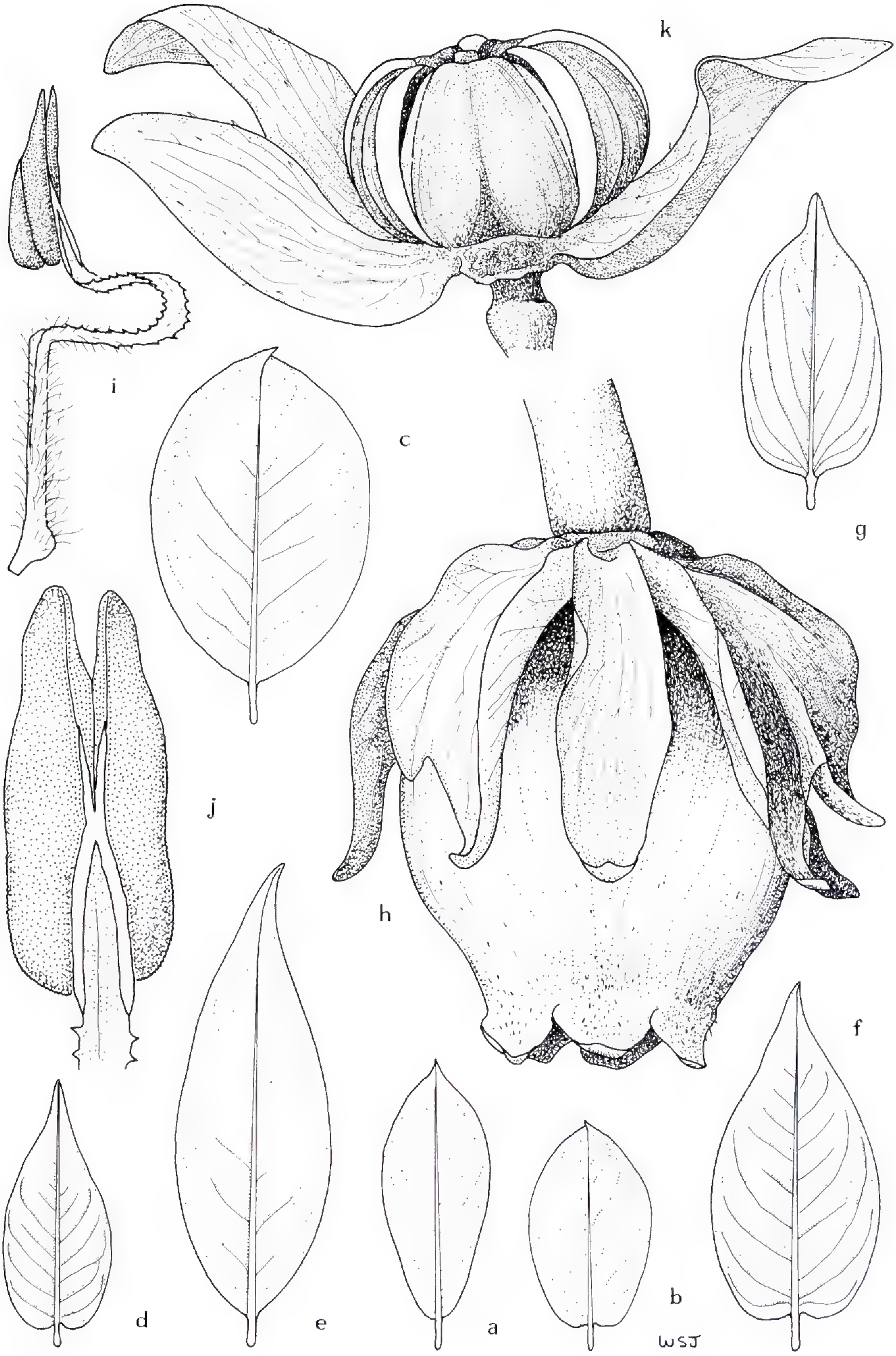


FIGURE 27. a–c, *Lyonia villosa* var. *pubescens* (in part), leaves, × .5. d–k, *L. macrocalyx:* d–g, leaves, × .5; h, flower, × 6; i, stamen, × 12.5; j, anther, × 25; k, capsule, × 6.

near Lanba, *Handel-Mazzetti 1665* (W); Omei Hsien, Mt. Omei, *Hu 8217* (US); Muli territory, between Baurong and Kulu, W. of Yalung R., *Rock 17813* (A, E, NY, US); Muti Konka, snow range E. of Yalung R., *Rock 23707* (A, E, K, NY, UC); prov. Batang, Yargong, *Soulie 3633* (P); near Wen-chuan Hsien, Wa-sen country, *Wilson 3191* (A); Wa-shan, *Wilson 3192* (A, E, K, US); NE. of Tachien-lu, *Wilson 4194* (A, E, K, US); Juei-she Hsien, *Yü 1023* (A); Lei-po Hsien, *Yü 3444* (E); Mu-li, Wa-chin, Wa-ti, *Yü 14702* (A). YUNNAN: Tali, Chicken-foot Mt., *Chen 2396* (E); NE. of Likiang, Tzai-koo Snow Mt., *Feng 2531* (A); Mekong-Salwin divide, 28°12′N., *Forrest 431* (E); E. flank of Lichiang Range, lat. 27°15′N., *Forrest 2442* (E); Tsekou, *Monbeig s.n.*, 20 July 1912 (B, F); Wei-se Hsien, *Tsai 59664* (A); Ta-li Hsien, *Wang 63206* (A); Nar-jou, Tsa-wa-rung, *Wang 66530* (A); A-tun-tze, Dokerla, *Yü 7963* (A, E); Chung-tien, Hsiaochungtien, *Yü 10957* (A); Wei-hsi, W. of Tungchuling, *Yü 10730* (E). TIBET: Kongbo prov., Tamnyen La, 29°20′N., 94°43′E., *Ludlow et al. 4925* (A, E); Pe, Tsangpo Valley, 29°31′N., 94°54′E., *Ludlow et al. 5166* (A, E); Kongbo prov., Molo, 28°45′N., 90°E., *Ludlow et al. 5660* (E); Lilung Chu, Tsangpo Valley, 20°N., 94°E., *Ludlow et al. 5695* (E); Pome prov., Showa La, *Ludlow et al. 13174* (A, E); Kongbo prov., Je, Pasum Tso, *Ludlow et al. 14083* (E); Kongbo prov., Deyang La, *Ludlow et al. 14301* (E). **Burma:** Adung Valley, *Ward 9540* (A). **Bhutan:** between Laya and Gyasa Dzong, Mo Chu, *Ludlow et al. 16480* (A, E).

Lyonia villosa is most closely related to the widespread and variable *L. ovalifolia,* which occurs chiefly at lower elevations (FIGURE 7). *Lyonia villosa* differs consistently from all varieties of *L. ovalifolia* in its lack of two spurs (or appendages) on the filament just below the anther-filament junction.

Populations of *Lyonia villosa* are separable into three morphologically distinct and geographically isolated varieties (MAP 8). These varieties are distinguished mainly by differences in the distribution of unicellular hairs, the size of the leaves, and the shape and size of the corollas (see key). As its name implies, *L. villosa* var. *pubescens* tends to have all its parts more densely covered with unicellular hairs than does either var. *villosa* or var. *sphaerantha.* Although it has been stated (for example, by Rehder, 1924) that this taxon can be differentiated from "typical" *L. villosa* by its pubescent ovary, this is often untrue. Some plants do, indeed, have unicellular hairs on the ovary, but others completely lack these hairs or have only a very few.

Of the three varieties of *Lyonia villosa,* var. *pubescens* is the most variable. Plants of this taxon collected from Bhutan and from extreme northern Burma, and some of those from southeastern Tibet, tend to have small leaves (to ca. 4.5 cm. long) that are quite wide in relation to their length, and small, urceolate to long-urceolate flowers. Such plants are superficially similar to *L. villosa* var. *sphaerantha* but can be easily separated by their moderate to dense covering of unicellular hairs on the pedicels and on the major veins (or at least the lower portion of the midvein) on the abaxial leaf surface. These forms intergrade completely with the more typical representatives of var. *pubescens* of Yunnan and Szechwan (i.e., plants with rather large leaves and more or less cylindrical flowers).

The ranges of *Lyonia villosa* vars. *sphaerantha* and *pubescens* overlap

in extreme northwestern Yunnan and adjacent Burma, where intermediate plants seem to be rather common (for example, see: Yunnan, Ta-li, *Delavay 1889* (F, in part), Lo-pin-chan, Lan-kong, *Delavay 4313* (A, US), Tsekou, *Soulier 1357* (A, F, L), Sung-kwei Pass, Lang-kong Valley, 26°12′N., *Forrest 5842* (E, K); Burma, Adung Valley, *Ward 9749* (A, in part)). These unusual plants have both papillae and unicellular hairs on their abaxial leaf surfaces and often have quite pubescent pedicels; they tend to have leaves and flowers intermediate in shape and size and seem to be completely fertile.

Lyonia villosa vars. *pubescens* and *sphaerantha* have probably both occasionally hybridized with *L. ovalifolia;* these hybrids are discussed under the latter taxon. I have seen no specimens intermediate between *L. villosa* var. *villosa* and *L. ovalifolia,* although Osmaston (1927) said that he found the two growing together at 9500 ft. at the head of the Nandagini Valley in Kumaon (India).

5. **Lyonia macrocalyx** (Anthony) Airy Shaw, Curtis's Bot. Mag. **160:** *t. 9490.* 1937.

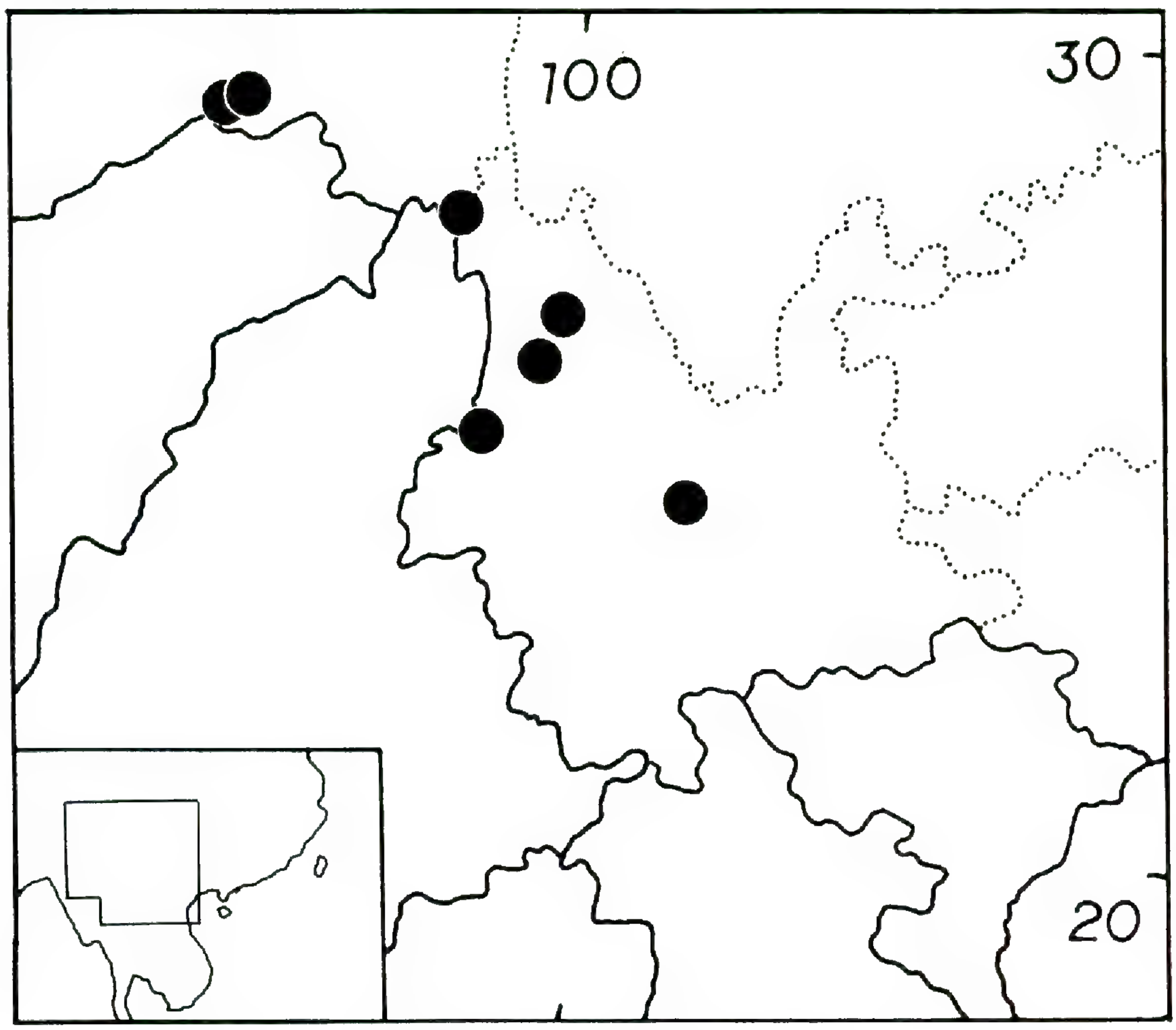
Pieris macrocalyx Anthony, Notes Roy. Bot. Gard. Edinburgh **15:** 241. 1927. TYPE: [China], prov. Yunnan, hills N. of Lung-fan, 25°54′N., 98°33′E., alt. 9000 ft., June 1925, *G. Forrest 26800* (holotype, E!; isotypes, A!, P!, S!, US!).

Semi-evergreen to deciduous shrub to ca. 3 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs terete to very slightly angled, slender, with few long-headed hairs, otherwise glabrous. Buds elongate-ovoid to ovoid, 1.5–10 by 1.5–4.5 mm. Leaf blades ovate to nearly elliptic, (3.5–)5–10.5(–13) by (1.5–)2.5–4(–5) cm., ± flat, slightly coriaceous, ca. 0.17–0.24 mm. thick; apex acuminate to long-acuminate; base ± broadly cuneate to slightly cordate; margin entire, plane to slightly revolute; venation eucamptodromous (rarely acrodromous, imperfect, suprabasal) to brochidodromous, 3° veins reticulate to percurrent; adaxial surface with sparse long-headed hairs, sparsely pubescent on midvein, otherwise glabrescent, with 3° and higher order veins obscure to visible, and 2° veins often slightly depressed; abaxial surface strongly papillose, glaucous, with long-headed hairs, otherwise glabrous, with 3° and higher order veins slightly and laxly reticulate, and 2° veins raised and visible, smoothly arching toward margin, or sinuous and ± irregular; petiole 2.5–10 mm. long, with long-headed hairs, otherwise glabrous or pubescent adaxially. Flower buds usually below vegetative buds; inflorescences racemose, to ca. 10-flowered, 0.5–5.5(–6.5) cm. long, slightly ascending; flowers pendulous and secund. Pedicels slender to moderately stout, 5–11 mm. long, often with long-headed hairs, otherwise glabrous; bracteoles opposite, basal, ovate, 1.5–6 mm. long; bracts 0.8–3 cm. long, 1 to 3 near base of raceme usually large and leaflike, the others small, similar to bracteoles, usually caducous. Flowers 5-merous, but calyx often variable; calyx lobes 5 (to 8) (due to partial and/or complete division of 1 or more lobes into a compound structure), persistent to occasionally deciduous, triangular to ovate, with acute or obtuse to acuminate apices, 4.5–9(–11)

by 1.5–5.5(–7) mm., the adaxial side usually with few long-headed hairs, otherwise glabrous, the abaxial side papillose and glaucous, with scattered long-headed hairs, otherwise glabrous; corolla urceolate to globose, 6.5–9 by 5–6.5 mm., white, abaxially with sparse long-headed hairs; filaments moderately to densely long-pubescent, especially near base, 4.5–6 mm. long, unappendaged, anthers 1.5–2 mm. long; ovary glabrous, placentae ± subapical. Capsule ± subglobose, 3–4.5 by 4–6 mm., glabrous, with pale, strongly thickened sutures that in dehiscence usually split irregularly and remain attached to an adjacent valve; seeds 0.7–1.5 mm. long. (FIGURE 27; see also Airy Shaw (1937), Stevens (1970).)

DISTRIBUTION AND ECOLOGY. China, chiefly northwestern portions of Yunnan and southeastern parts of Tibet, probably also in northern Burma (MAP 9). Mountainous areas, forests, open scrub vegetation of rocky slopes; ca. 1900–3300 m. alt. Flowering chiefly May to July.

REPRESENTATIVE SPECIMENS. **China.** TIBET: Trulung, Po Tsangpo, Pome, *Ludlow et al. 13029* (E); Tsangpo Gorge, *Ward 6317* (E, K); Taron-Taru divide, Lungnan to Tehgai, *Yü 20885* (A, E). YUNNAN: Salwin–Kui-chiang divide, 27°15′N., 98°40′E., *Forrest 25567* (E, K, US, W); N. of Lung-fan, 25°54′N., 98°33′E.,



MAP 9. Distribution of *Lyonia macrocalyx* (Yunnan and Tibet).

Forrest 27741 (A, E, W); Shang-pa Hsien, *Tsai 54886* (A); Laktang, *Ward 3226* (E).

Lyonia macrocalyx, a distinctive and beautiful plant, can easily be recognized by its subfoliaceous, elongate, and usually greatly expanded calyx lobes; its large, urceolate corollas; its unappendaged filaments; and its coriaceous, semi-evergreen leaves with the apex long-acuminate, the major veins on the adaxial surface often slightly depressed, and the abaxial surface papillose and glaucous. It is readily distinguished from its nearest allies, *L. villosa* and the variable *L. ovalifolia,* by the characters given above. Although these three taxa have overlapping geographic ranges, it is not known whether they ever occur together.

Occasionally the secondary veins arising from near the base of the leaf blade are so strongly developed that a nearly plinerved condition occurs.

Lyonia Nutt. sect. ARSENOCOCCUS (Small) Judd, comb. nov.

Arsenococcus Small in Small & Carter, Fl. Lancaster Co. 218. 1913. *Xolisma* Raf. sect. *Arsenococcus* (Small) Rehder, Jour. Arnold Arb. **5:** 54. 1924. TYPE SPECIES: *Lyonia ligustrina* (L.) DC.

Deciduous shrubs, often spreading by horizontal underground rhizomes, the branches with heterogeneous pith. Indumentum of unicellular hairs and multicellular, biseriate-stalked, extremely long-headed hairs. Buds with 2 large, imbricate scales. Leaves serrulate, with unlignified or only slightly lignified epidermis, lacking hypodermis. Flowers usually 5-merous, in small panicles; calyx lobes valvate in bud; corolla urceolate; filaments with ± long, unicellular hairs near base, with pair of small spurs below junction with anthers; placentae positioned subapically on columella. Capsules with pale, ± moderately thickened sutures, usually adhering to valve or splitting irregularly in dehiscence; seeds oblong-ovoid to spindle shaped, ends sometimes truncated.

DISTRIBUTION. United States: Coastal Plain, Piedmont, and mountains; Maine, south to Florida, west to eastern Texas, Arkansas, and Oklahoma.

NUMBER OF SPECIES (TAXA). 1 (2).

6. **Lyonia ligustrina** (L.) DC. Prodr. **7:** 599. 1839.

Deciduous to semi-evergreen shrub to ca. 4 meters tall, with grayish, shallowly and longitudinally furrowed bark; often spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly angled, slender, sometimes turning reddish in autumn, with scattered long-headed hairs, otherwise glabrous to densely pubescent. Buds elongate-ovoid, 1–4 by 0.5–1.8 mm., often red in autumn. Leaf blades narrowly to widely elliptic, obovate, or ovate, (1.5–)2–9.5(–10.5) by 1–4.5(–5) cm., ± flat, chartaceous to slightly coriaceous, ca. 0.15–0.26 mm. thick, often turning reddish in autumn; apex acute to acuminate or mucronate; base attenuate, narrowly to broadly cuneate or rounded; margin clearly to minutely serrulate, plane to slightly revolute; venation brochidodromous, with 3° veins reticulate to ± percurrent; adaxial

surface with sparse to dense long-headed hairs (these sometimes deciduous with age), sparsely to densely pubescent on midvein, especially proximal portion, and sometimes also on 2° veins, with 3° and higher order veins obscure to slightly visible, and 2° veins usually not depressed; abaxial surface with sparse to dense long-headed hairs, otherwise glabrous to densely pubescent on midvein and sometimes on 2° (or even 3°) veins, the 3° and higher order veins obscure to slightly visible and 2° veins slightly to strongly raised, sinuous to straight or slightly curved toward apex; petiole 1–8 mm. long, with long-headed hairs, otherwise pubescent adaxially or all around. Flower buds usually above vegetative buds; inflorescences racemes of fascicles to racemes of short racemes, to 15- to 45- (to 60-)flowered, 0.5–6(–9) cm. long, horizontal to slightly ascending. Pedicels usually slender, (1–)2–10 mm. long, with long-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to linear, 0.2–1.3 mm. long, often caducous; bracts all very small and similar to bracteoles in shape, or with very few to many large and leaflike, to 3 cm. long, and others small and caducous. Flowers usually 5-merous; calyx lobes triangular, with acuminate apices, 0.5–1.5 by 0.4–1 mm., the adaxial side glabrous, the abaxial side with scattered long-headed hairs, otherwise glabrous to densely pubescent; corolla urceolate, 2–4(–4.5) by 2–4.5 mm., white, abaxially with sparse to dense long-headed hairs, rarely also sparsely pubescent; filaments with long-unicellular hairs near base, 1–2 mm. long, with 2 short spurs below anther-filament junction, anthers 0.6–1.2 mm. long; ovary densely covered with long-headed hairs, often otherwise pubescent, placentae ± subapical. Capsules globose to subglobose, 2–3 by 2–4 mm., usually with sparse to dense long-headed hairs, otherwise glabrous to moderately pubescent, with pale, much-thickened sutures that in dehiscence remain attached to an adjacent valve; seeds 0.7–1.7 mm. long.

DISTRIBUTION. United States (Maine to Florida, west to Arkansas, Texas, and Oklahoma); various habitats of mountains, Piedmont, and Coastal Plain; near sea level to nearly 2000 m. alt.

COMMON NAMES. Maleberry, he-huckleberry, male-huckleberry, male-blueberry, seedy-buckberry.

Key to Varieties of *Lyonia ligustrina*

1. Inflorescences naked or with only few foliaceous bracts, [mountains and Piedmont south of Virginia; mountains, Piedmont, and Coastal Plain north of Virginia] . . . . . 6a. var. *ligustrina.*
1. Inflorescences with conspicuously foliaceous bracts or at least lower inflorescences with large bracts, [Coastal Plain from southeastern Virginia to Florida, west to eastern Texas, Oklahoma, and Arkansas (mountains)] . . . . . 6b. var. *foliosiflora.*

6a. **Lyonia ligustrina** (L.) DC. var. **ligustrina**

Vaccinium ligustrinum L. Sp. Pl. 351. 1753. *Andromeda ligustrina* (L.) Muhl. Catal. Pl. Am. Sept. 44. 1813. *Xolisma ligustrina* (L.) Britton, Mem. Torrey Bot. Club **4:** 135. 1894. *Arsenococcus ligustrinus* (L.) Small

in Small & Carter, Fl. Lancaster Co. 218. 1913. *Lyonia ligustrina* (L.) DC. var. *typica* Fern. Rhodora **43:** 625. 1941. TYPE: "in Pennsylvania," *Kalm s.n.* (lectotype, LINN, sheet no. 497.11, microfiche photo seen).

Andromeda paniculata L. var. *nudiflora* Michaux, Fl. Bor. Am. **1:** 255. 1803. TYPE: Pennsylvania, *A. Michaux s.n.* (lectotype, P-MICHX (IDC 6211. 58: I. 7!)).

Deciduous shrub. Buds glabrous to sparsely pubescent. Leaf blade ± chartaceous. Pedicels (1–)2–7.5 mm. long; bracts all very small and similar to the bracteoles (occasionally very few larger and leaflike, to 0.5–1.5(–2) cm. long), often quickly deciduous; inflorescences not conspicuously leafy. Corolla 2–4(–4.5) by 2–4.5 mm. (FIGURE 28; see also Watson (1825, *t. 37.*, as *L. paniculata*); Britton & Brown (1913); Gleason (1952); Graves (1952); Braun (1961); Radford, Ahles, & Bell (1968); Campbell & Hyland (1975, *pl. XLVIII, 2.*)

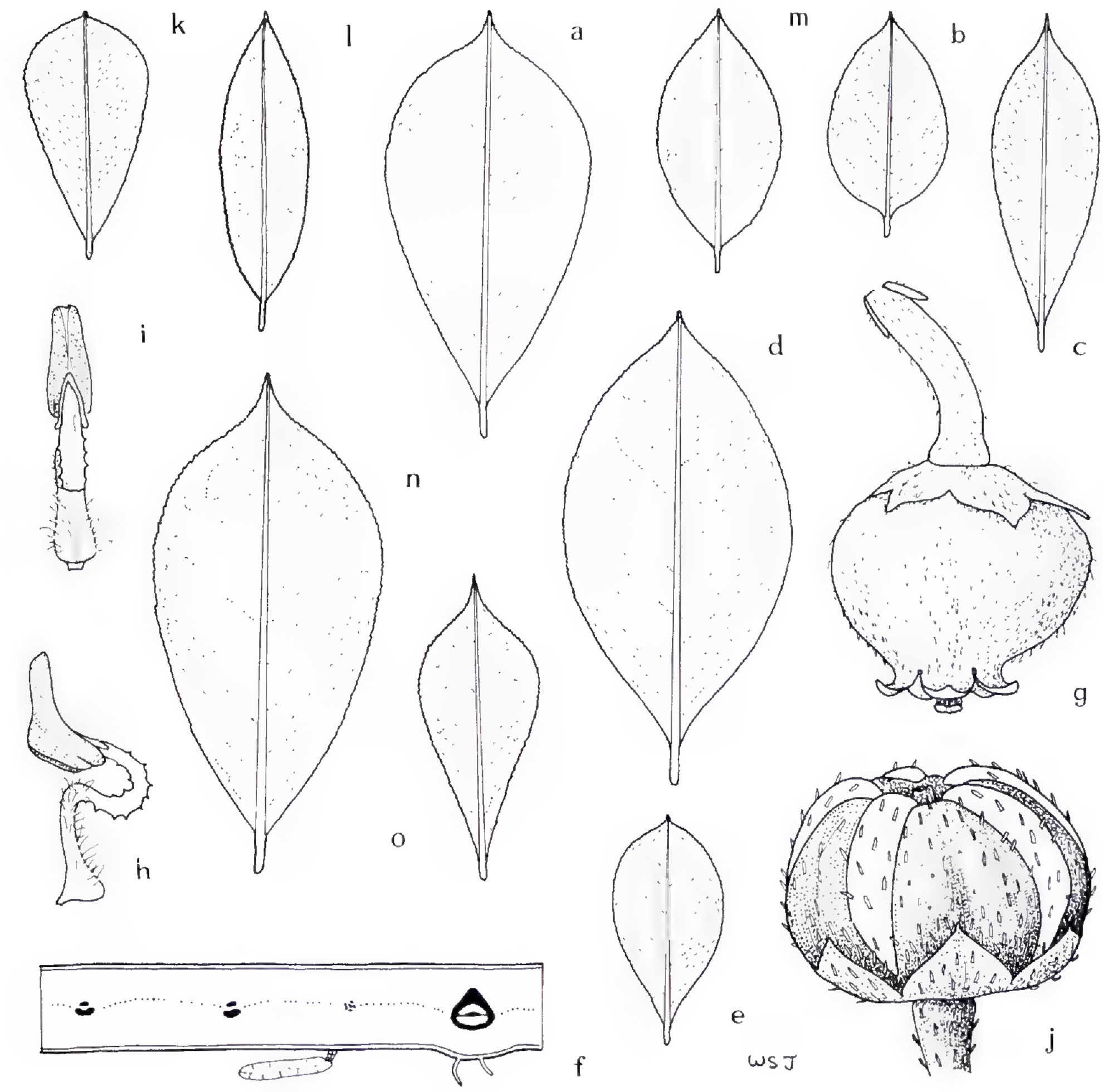
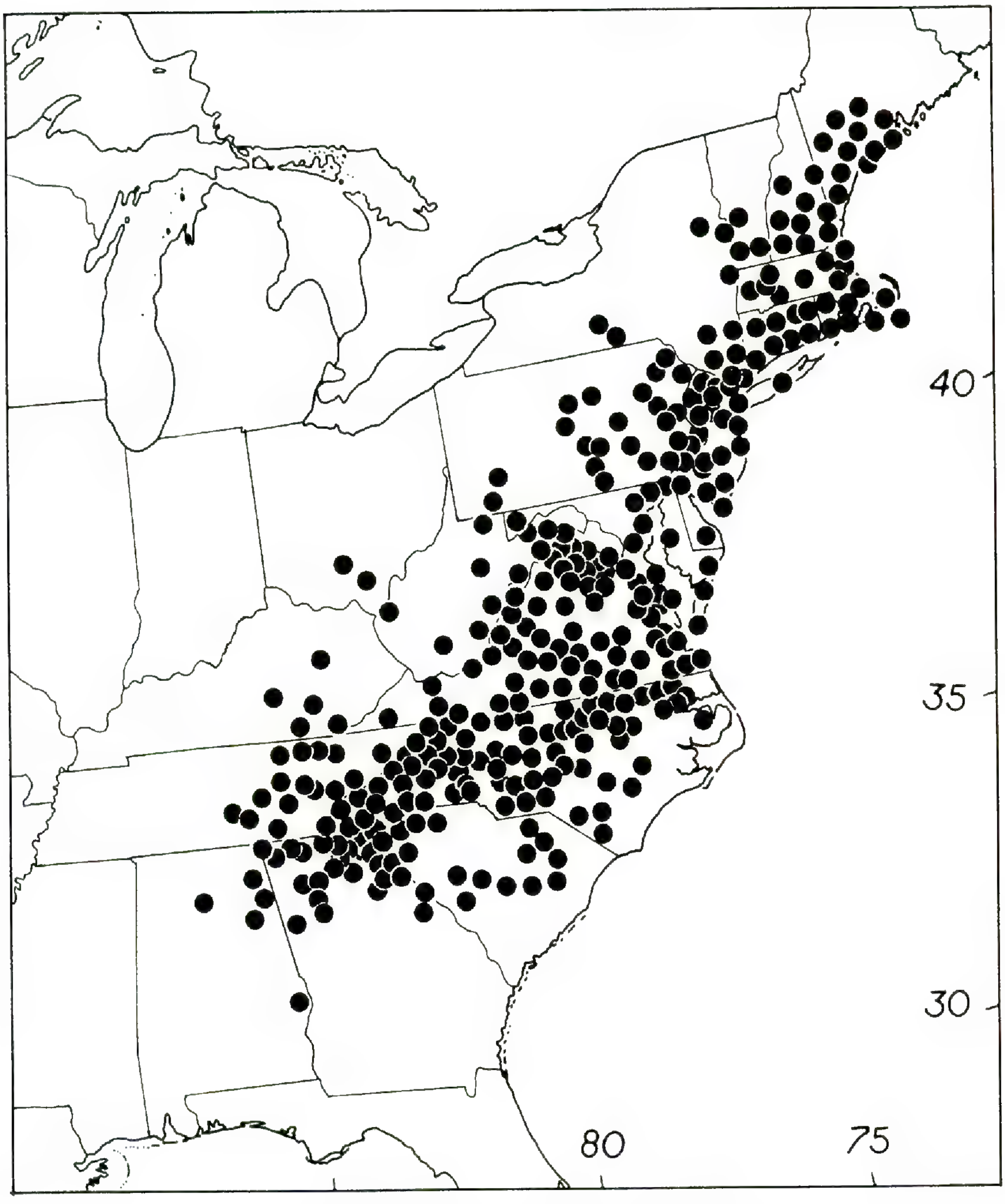


FIGURE 28. a–j, *Lyonia ligustrina* var. *ligustrina:* a–e, leaves, × .5; f, cross section of leaf blade, × 50; g, flower, × 6; h, i, stamens, × 12.5; j, capsule, × 6. k–o, *L. ligustrina* var. *foliosiflora,* leaves, × .5.

DISTRIBUTION AND ECOLOGY. United States (South Carolina, northern Georgia and Alabama, to Maine); mountains, Piedmont, and Coastal Plain (MAP 10). Moist to dry acid woods and thickets, forest-, pond-, swamp-, or river-margins, grassy and/or heath balds, acid swamps and bogs; sea level to nearly 2000 m. alt. Especially prevalent in *Acer rubrum* swamps, *Pinus* and/or *Quercus* woods, and thickets of *Vaccinium*, *Rhododendron*, or other ericads. Flowering late April through early July, varying greatly with latitude and elevation.

REPRESENTATIVE SPECIMENS. **United States.** MAINE. Knox Co.: S. shore of Newbert Pond, Appleton, *Rossbach 1557* (NCU). Oxford Co.: Lovell, *Johnson 111* (NY).



MAP 10. Distribution of *Lyonia ligustrina* var. *ligustrina*.

Somerset Co.: near Pittsfield, *Knight 1840* (GH). York Co.: 0.75 mi. N. of Bauneg Beg Pond, *True 5147* (GH). NEW HAMPSHIRE. Cheshire Co.: near E. Jaffrey, *Palmer 43033* (A). Grafton Co.: E. Hebron, *Nelson s.n.*, 10 July 1917 (NY). Merrimack Co.: Hooksett, *Batchelder s.n.*, 16 July 1921 (NEBC). Rockingham Co.: Fox Hill Point, N. Hampton, *Harris 20991* (NEBC). VERMONT. Bennington Co.: Pownal, *Eggleston 1424* (NY). Rutland Co.: Tadmire Hill, Pawlet, *Dutton 1175* (A). MASSACHUSETTS. Barnstable Co.: near Orleans, *Palmer 44807* (GH). Berkshire Co.: Mt. Washington, *Moldenke 11651* (NY). Middlesex Co.: near Long Bridge, Newton, *Gilbert s.n.*, 19 June 1894 (GH). Nantucket Co.: Polpis, Nantucket Is., *MacKeever N532* (NY). Worcester Co.: Pine Hill, Lancaster, *Brown s.n.*, 20 August 1942 (TEX). RHODE ISLAND. Newport Co.: Newport, *Mearns 611* (NY). Providence Co.: near Harrisville, *Palmer 44967* (A). CONNECTICUT. Fairfield Co.: near New Canaan, *Harger 7684* (GH). Hartford Co.: Southington, *Andrews s.n.*, 26 August 1903 (GH). New London Co.: near Stonington, *Harger 6310* (NCU). NEW YORK. Dutchess Co.: near Clove, *Standley & Bollman 11908* (US). Orange Co.: Black Rock Forest, *Raup 7805* (GH). Rensselaer Co.: Sandlake, *House 5181* (NY). Suffolk Co.: Hauppauge Bog, Cold Spring Harbor, *Cain 484* (NY). Tompkins Co.: South Hill, Ithaca, *Eames & Thomas 4770* (GH). Warren Co.: 2 mi. S. of Luzerne, *Fogg 19209* (NY). PENNSYLVANIA. Adams Co.: 5.75 mi. WSW. of Wenksville, *Tanger 4381* (DUKE). Bucks Co.: 2.5 mi. NW. of Neshaminy, *McDowell 395* (GH). Centre Co.: 1 mi. W. of Hublersburg, *Wahl 520* (GH). Fayette Co.: Ohiopyle, *Bright 16920* (TEX). Juniata Co.: Tuscarora Mt., 3.5 mi. S. of Port Royal, *Adams 5237* (A). Luzerne Co.: along Susquehanna R. above Nescopec, *Heller 14215* (A). NEW JERSEY. Bergen Co.: Franklin Lakes, *Moldenke 10745* (NY). Cape May Co.: 2 mi. SE. of Goshen, *Lems s.n.*, June 1962 (MSC). Gloucester Co.: Riders Bog, near Nialaga, *Bassett s.n.*, 23 August 1923 (GH). Ocean Co.: 2 mi. E. of Cedar Grove, *Fogg 4849* (GH). Sussex Co.: 1–2 mi. N. of Sparta, *Adams & Wherry 1541* (A). DELAWARE. New Castle Co.: Highland Woods off Darley Rd., *Reed 51105* (MSC). Sussex Co.: 4 mi. W. of Rehoboth Beach, near Love Creek, *McVaugh 6545* (GH, NY). DISTRICT OF COLUMBIA: Takoma Park, *Painter 304* (DUKE). MARYLAND. Charles Co.: Wolfden Creek, Cedarville State Forest, *Simpson s.n.*, 5 July 1952 (US). Garrett Co.: Mt. Lake Park, *Shreve 540* (US). Hartford Co.: 0.5 mi. SSW. of Havre de Grace, *Shull 157* (NY). Talbot Co.: Miles Creek, 2 mi. NE. of Trappe, *Earle 1693* (GH). Worcester Co.: along edge of Corker's Creek, 4 mi. S. of Snow Hill, *Judd 33* (MSC). VIRGINIA. Albemarle Co.: at Albemarle-Nelson county line on Va. 6, *James 12136* (NCU). Fauquier Co.: 3 mi. below Thorofare Gap, Pond Mt., *Allard 11329* (GH). Isle of Wight Co.: near Franklin, *Heller s.n.*, 7–28 June 1893 (A). King William Co.: banks of Mattaponi R. near King William Landing, *Fernald & Long 11601* (GH, NY). Mecklenburg Co.: E. of Boydton, *Gleason 8690* (NY). Pittsylvania Co.: NE. of Kentuck, *James 3192* (NCU). Pulaski Co.: NW. of Pulaski, *James 8509* (NCU). Rockingham Co.: above Hone Quarry Camp, *Allard 2114* (US). Scott Co.: 2.5 mi. E. of jct. of U.S. 58 and Co. Rd. 701, *James 9660* (NCU). WEST VIRGINIA. Cabell Co.: Rickett's Place, *Gilbert 556* (FSU, DUKE, GH, NY, US). Greenbrier Co.: White Sulphur Springs, *Hunnewell 6747* (GH). Hampshire Co.: Campon Springs, *Hunnewell 17984* (GH). Pendleton Co.: Shenandoah Mt., near U.S. 33, *Radford 45912* (NCU). Upshur Co.: Buckhannon, *Millspaugh 411* (NY). NORTH CAROLINA. Alamance Co.: 18.7 mi. W. of Chapel Hill, *Radford & Rabb 714* (NCU). Ashe Co.: 4 mi. NE. of Jefferson, *Radford 6233* (NCU). Buncombe Co.: near Biltmore, *Biltmore Herbarium 26* (GH, NCU, NY). Cherokee Co.: 1 mi. SE.

of Unaka, *Radford 17591* (NCU). Duplin Co.: 5.5 mi. N. of Beulaville, *Ahles 24084* (NCU). Iredell Co.: 4 mi. ENE. of Harmony, *Ahles 45222* (NCU). Macon Co.: N. of Highlands, *Godfrey 51465* (FSU). Northampton Co.: 2.1 mi. WNW. of Garysburg, *Ahles 45592* (NCU). Richmond Co.: along Drowning Creek, on U.S. 1 just S. of Moore Co. line, *Fox 3671* (GH). Wake Co.: Lake Johnson, *Godfrey 49403* (GH). SOUTH CAROLINA. Aiken Co.: 1.3 mi. W. of jct. of U.S. I-76 and S.C. 254, *Ahles 55471* (NCU). Clarendon Co.: 3 mi. SW. of Manning, *Godfrey & Tryon 906a* (GH, NY). Florence Co.: 1.8 mi. WSW. of Hyman, *Bell 7563* (NCU). Greenville Co.: above River Falls, *Rodgers & Mullens 67211* (NCU). Oconee Co.: 7 mi. NW. of Jocassee, *Radford 17725* (NCU). Spartanburg Co.: N. of Spartanburg, *Bell 8343* (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, *Greear 64417* (GA, NCU). Carroll Co.: 8.5 mi. N. of Carrolton, *Carnes 66* (GA). Clarke Co.: near Athens, *Harper s.n.*, 2 June 1897 (NY). Dade Co.: summit of Lookout Mt., *McVaugh 9043* (NCU, TEX). Madison Co.: ca. 6 mi. from Ida, *Montgomery 445* (GA). McDuffie Co.: near Thomson, *Bartlett 1653* (NCU, VDB). Rabun Co.: Tallulah Falls, *Perry & Straham 976* (NY). Whitfield Co.: Taylor's Ridge, *Wilson 152* (NY). OHIO. Ross Co.: Liberty Twp., near Jones' Crossing, *Bartley & Pontius 92* (NY). KENTUCKY. Bell Co.: near Middlesboro, *Gleason 8828* (NY). Laurel Co.: near Corbin, *Horsey 2265* (GH). McCreary Co.: S. fork of Cumberland R., *Braun 1016* (US). Powell Co.: Stanton, *McFarland 2398* (US). TENNESSEE. Blount Co.: top of Gregory's Bald, *Wilson 1783* (GH). Campbell Co.: near Pioneer, *Sharp et al. 3828* (NCU). Carter Co.: near Roan Mt., *Rehder s.n.*, 20 June 1900 (A). Coffee Co.: Manchester, *Godfrey 69807* (FSU, NCU). Cumberland Co.: W. of Crossville, *Kral 40544* (VDB). Hamilton Co.: Walden Ridge, above Soddy, *Underwood & Sharp 2357* (NCU). Van Buren Co.: near Piney Creek Falls, *Shanks et al. 4505* (NCU). ALABAMA. Calhoun Co.: 9.1 mi. NNE. of Jacksonville, *Clark 16039* (NCU). Cherokee Co.: Little River Canyon Park, *Kral 33351* (FSU, VDB). DeKalb Co.: DeSoto State Park, near Ft. Payne, *Kral 36502* (VDB). Russell Co.: ca. 2 mi. W. of Phenix City, *Duncan 9636* (GA, MO).

6b. **Lyonia ligustrina** (L.) DC. var. **foliosiflora** (Michaux) Fern. Rhodora **10:** 53. 1908.

Andromeda paniculata L. var. *foliosiflora* Michaux, Fl. Bor. Am. **1:** 255. 1803. *Andromeda frondosa* Pursh, Fl. Am. Sept. 295. 1814, *nomen novum*. *Lyonia frondosa* (Pursh) Nutt. Gen. N. Am. Pl. **1:** 267. 1818. *Andromeda ligustrina* (L.) Muhl. var. *frondosa* (Pursh) Wood, Class Book, 488. 1861. *Andromeda ligustrina* (L.) Muhl. var. *pubescens* Gray, Synopt. Fl. N. Am. **2:** 33. 1878, *nomen superfluum*. *Andromeda paniculata* L. var. *pubescens* (Gray) Dippel, Handb. Laubholzk. **1:** 370. 1889. *Xolisma ligustrina* (L.) Britton var. *foliosiflora* (Michaux) Mohr, Bull. Torrey Bot. Club **24:** 24. 1897. *Xolisma foliosiflora* (Michaux) Small, Fl. SE. U.S. 889. 1903. *Andromeda ligustrina* (L.) Muhl. var. *foliosiflora* (Michaux) Fern. in Robinson & Fern. Gray's Man. ed. 7. 635. 1908. *Xolisma ligustrina* (L.) Britton var. *pubescens* (Gray) Millsp. Liv. Fl. W. Virginia 324. 1913. *Arsenococcus frondosus* (Pursh) Small, Shrubs Florida, 97. 1913. *Lyonia ligustrina* (L.) DC. var. *pubescens* (Gray) Bean, Trees Shrubs Brit. Isles **2:** 64. 1914. (*Lyonia ligustrina pubescens* Rehder in Bailey, Cycl. Am. Hort. **1:** 62. 1900, without citation of basionym or designation of rank). TYPE: United States, "in stagnosis," *A. Michaux s.n.* (lectotype, P-MICHX (IDC 6211. 58: II. 2!); duplicate of lectotype?, P!).

Andromeda parabolica Veillard in Duhamel, Traité Arbres Arbustes, ed. 2 (Nouv. Duhamel). 191. [1800–] 1801–1819 (but this description probably published ca. 1803). *Lyonia parabolica* (Veillard) Koch, Dendrol. **2:** 199. 1872. TYPE: "l'Amérique septentrionale, dans la Georgie et la Floride" (not seen).

Andromeda tomentosa Dum.-Cours. Bot. Cult. ed. 2. **3:** 495. 1811. *Andromeda paniculata* L. var. *tomentosa* (Dum.-Cours.) Dippel, Handb. Laubholzk. **1:** 369. 1889. TYPE: (not seen).

Lyonia salicifolia Watson, Dendr. Brit. **1:** *t. 38.* 1825. *Lyonia ligustrina* (L.) DC. var. *salicifolia* (Watson) DC. Prodr. **7:** 600. 1839. *Andromeda watsoniana* Steudel, Nomencl. Bot. ed. 2. **1:** 89. 1840, *nomen novum.* TYPE: "Place . . . Arboretum, Kew. Country . . . North America" (not seen).

Lyonia capreifolia Watson, Dendr. Brit. **2:** *t. 127.* 1825. *Lyonia ligustrina* (L.) DC. var. *capreifolia* (Watson) DC. Prodr. **7:** 600. 1839. TYPE: "Place . . . Mr. James Lee's, Hammersmith. Country . . . North America" (not seen).

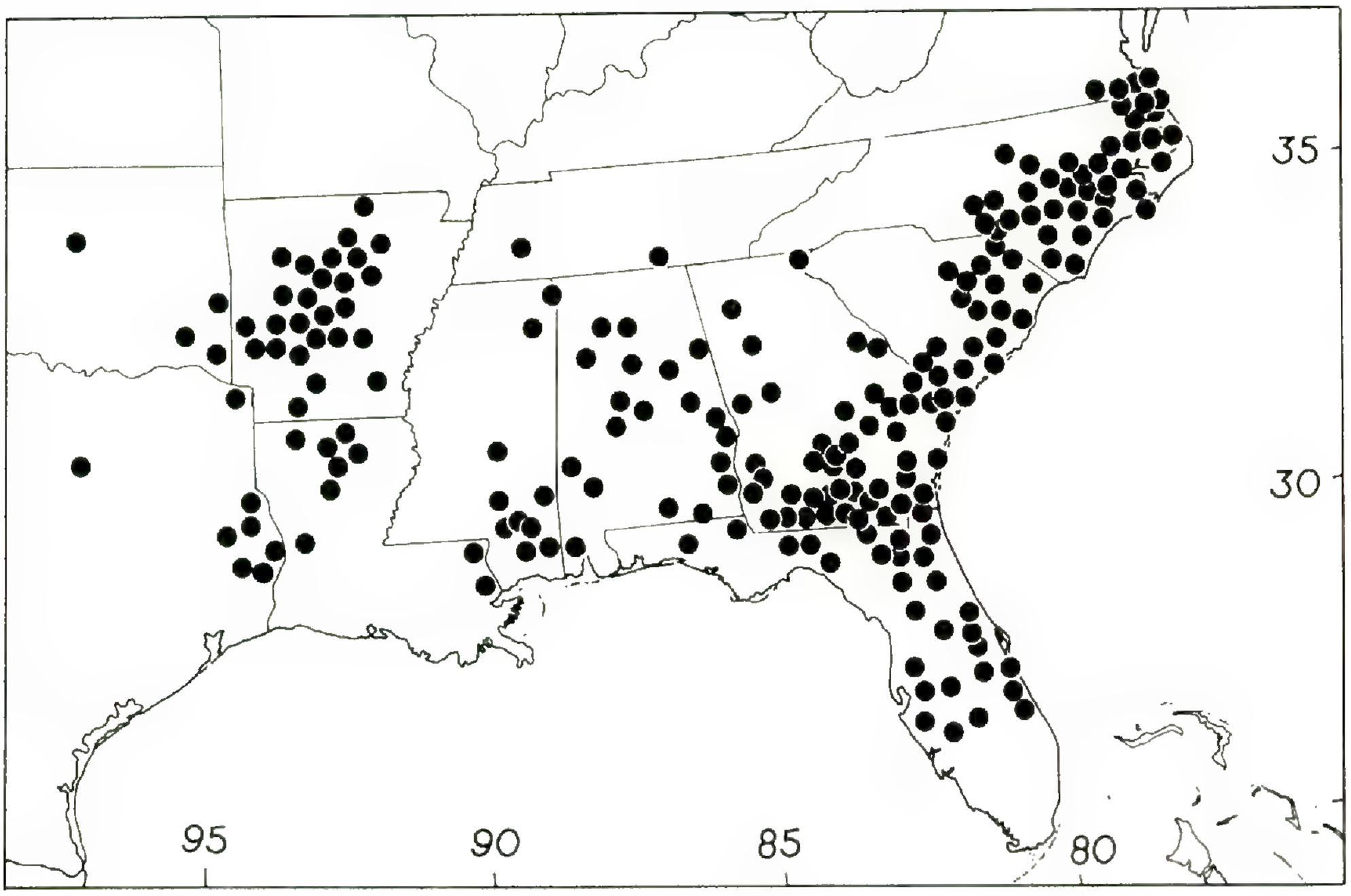
Lyonia multiflora Watson, Dendr. Brit. **2:** *t. 128.* 1825. *Andromeda polyantha* Steudel, Nomencl. Bot. ed. 2. **1:** 89. 1840, *nomen novum.* TYPE: "Place . . . Mr. James Lee's, Hammersmith. Country . . . North America" (not seen).

Lyonia ligustrina (L.) DC. f. *nanella* Fern. Rhodora **163:** 158. 1947. TYPE: United States, Virginia, Nansemond Co., sphagnous and peaty bog by Norfolk and Western Railway about 0.5 mi. W. of Kilby, 8 and 12 Sept. 1946, *Fernald, Long, & Clement 15331* (holotype, GH!; isotype, US!).

Deciduous to semi-evergreen shrub. Buds glabrous to densely pubescent. Leaf blades ± chartaceous to slightly coriaceous. Pedicels 2.5–10 mm. long; bracts variable, many large and leaflike, to 0.5–3 cm. long, others small and similar to bracteoles, sometimes quickly deciduous; inflorescences conspicuously leafy, or at least lower inflorescences with large bracts. Corolla 2–3.5 by 2–4 mm. (FIGURE 28; see also Watson (1825, *t. 38* as *L. salicifolia, t. 127* as *L. capreifolia, t. 128* as *L. multiflora*); Vines (1960); and D. S. & H. B. Correll (1972).)

DISTRIBUTION AND ECOLOGY. United States, Atlantic Coastal Plain from southeastern Virginia to Florida, west to Arkansas, eastern Texas, and southeastern Oklahoma (MAP 11). Moist pine forests or flatwoods, acid thickets, shrub-bogs, marshy areas, stream-, pond-, or swamp-margins, *Taxodium* or *Chamaecyparis* swamps, swamps dominated by various broadleaved trees; near sea level to ca. 300 m. alt. Flowering late April through early July.

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA. Chesapeake Co.: Lake Drummond, Great Dismal Swamp, W. of Wallaceton, *Fernald & Long 13411* (GH). Nansemond Co.: E. of Cox Landing, *Fernald & Long 10765* (DUKE, GH). Southampton Co.: ca. 7 mi. S. of Franklin, *Fernald & Long 10006* (GH). NORTH CAROLINA. Beaufort Co.: 0.5 mi. N. of Wilmar, *Fox 4954* (NY). Bladen Co.: S. of Garland, *Blomquist s.n.*, 9 May 1951 (DUKE). Brunswick Co.: 7 mi. N. of Southport, *Wilbur 6715* (DUKE, TEX). Camden Co.: 1.3 mi. SW. of South Mills, *Lems s.n.*, 23 May 1959 (MSC). Carteret Co.: Harker's



MAP 11. Distribution of *Lyonia ligustrina* var. *foliosiflora*.

Is., *Smith s.n.*, 10 May 1942 (NCU). Dare Co.: U.S. 264 near Mann's Harbor, *Radford 8196* (NCU). Harnett Co.: 1 mi. SE. of Pineview, *Wilbur 9110* (DUKE). Onslow Co.: 3.7 mi. WSW. of Haw, *Ahles 28174* (NCU). Orange Co.: 12 mi. NW. of Chapel Hill, *Wiegand & Manning 2393* (GH). SOUTH CAROLINA. Berkeley Co.: 8 mi. SW. of Monock's Corners, *Godfrey & Tryon 1405* (GH). Darlington Co.: Hartsville, *Smith s.n.*, 10 June 1942 (NCU). Florence Co.: 3 mi. W. of Cowards, *Bell 10864* (NCU). Horry Co.: Myrtle Beach, *Coker s.n.*, 12 July 1945 (NCU). Jasper Co.: Ridgeland, *Ahles 12306* (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, *Greear 63104* (GA). Berrien Co.: W. of Ray City, *Bozeman 4748* (NCU). Charlton Co.: W. of Chessar's Is., Okefenokee Swamp, *Duncan 2007* (NY). Chatham Co.: Savannah, *Nuttall s.n.* (GH). Decatur Co.: 3 mi. W. of Faceville, *Thorne 4792* (NY). Lowndes Co.: 10 mi. ESE. of Valdosta, *Faircloth 4767* (NCU). McIntosh Co.: 1.3 mi. NE. of Ft. Barrington, *Bozeman 2354* (NCU). Screven Co.: near Cameron, *Reade E1625* (GA). Telfair Co.: 3 mi. NW. of Lumber City, *Wilbur 3152* (GA). FLORIDA. Alachua Co.: near Devil's Millhopper, *Wiggins 19754* (NCU, FLAS). Jefferson Co.: near Lloyd, *Godfrey 61426* (FSU). Hamilton Co.: 6 mi. E. of Jasper, *Godfrey 58511* (FSU, GH, VDB). Highlands Co.: Sebring, *Harbison 17* (A, NCU). Jackson Co.: 5 mi. E. of Marianna, *Hood & West 2022* (FLAS). Lake Co.: near Eustis, *Nash 528* (A, MSC, US). Nassau Co.: 6 mi. S. of Callahan, *Will & Ward s.n.*, 17 June 1961 (FLAS). Seminole Co.: N. of Goldenrod, *Cooley et al. 7404* (NCU). TENNESSEE. Franklin Co.: near Tallahoma, *Alexander et al. s.n.*, 24 Sept. 1933 (NY). Madison Co.: Jackson, *Bain 426* (NY). ALABAMA. Chilton Co.: 6.6 mi. NE. of Clanton, *Clark 17637* (NCU). Clark Co.: 6 mi. S. of Thomasville School, *Kral 41107* (VDB). Covington Co.: 17 mi. SSE. of Andalusia, *Duncan 15013* (NCU). Cullman Co.: St. Bernard, *Wolf s.n.*, 29 May 1922 (NCU). Henry Co.: 8 mi. N. of Headland, *Wiegand & Manning*

2396 (GH). Mobile Co.: near Mobile, *Mohr s.n.*, 13 May 1893 (A). Talladega Co.: along Salt Creek, T. 16 S., R. 8 E., *Clark 2844* (NCU). Winston Co.: Camp McDowell, along Clear Creek, *Clark 12969* (NCU). MISSISSIPPI. Covington Co.: S. of Hot Coffee, *Jones 2859* (GA). Forrest Co.: Hattiesburg, *Jones 2859* (GA). George Co.: along Hwy. 98, 0.5 mi. W. of Alabama-Mississippi state line, *Lelong 5200* (NCU). Tishomingo Co.: 6 mi. NE. of Iuka, *Ray 7522* (GH, MISSA, NCU). Wayne Co.: 5 mi. SE. of Shubata, *Ray 7004* (FSU, GH, MISSA, NCU). ARKANSAS. Drew Co.: near Monticello, *Demaree 13514* (NY). Hot Springs Co.: near Bismark, *Demaree 17415* (GH, NY). Ouachita Co.: near Stephens, *Demaree 16837* (NY). Pike Co.: near Langley, *Demaree 9517* (GH, NY). Pope Co.: Crow Mt., Galla Creek woods, *Tucker 7215* (NCU). Saline Co.: 2 mi. E. of Benton, *Demaree 35602* (NCU, VDB). Stone Co.: Ozark Natl. Forest, near Fiftysix, *Demaree 58226* (NCU, VDB). White Co.: about 0.5 mi. W. of Rosebud, *Redfearn 19239* (NCU). LOUISIANA. Ouachita Co.: Sec. 9, T. 17 N., R. 2 E., Tiger Branch off La. 838, *Thomas 11031* (VDB). Vernon Co.: about 2.5 mi. N. of Burr Ferry, *Thieret 27322* (DUKE, FSU). Washington Co.: 3 mi. NE. of Franklinton, *Correll 9198* (DUKE, GH). Webster Co.: 4 mi. W. of Minden, *Correll 10270* (DUKE, GH, NY). Winn Co.: 4 mi. W. of Winnfield, *Correll 10039* (DUKE, GH, NY). OKLAHOMA. LeFlore Co.: near Page, *Blakley 1427* (GH, US). Logan Co.: Jacks Creek camp, Strickland, *Demaree 15753* (NY). McCurtain Co.: 1.5 mi. SW. of Smithville, *Redfearn 19806* (NCU). Pushmataha Co.: along Little R., Honobia, *Waterfall 13023* (GH, US). TEXAS. Angelina Co.: N. edge of Boykin Springs, *Correll 16501* (GH). Bowie Co.: near Texarkana, *Heller 4178* (GH, NY). Newton Co.: E. of Newton, *Lundell 11881* (TEX). San Augustine Co.: San Augustine, *Palmer 10646* (A). Shelby Co.: 9.5 mi. SW. of Center, *McVaugh 8435* (GH, TEX). Tyler Co.: 6 mi. E. of Woodville, *Kral 29090* (ENCB, VDB).

Lyonia ligustrina is a rather isolated species, which is here placed in the monotypic section ARSENOCOCCUS, and is most closely related to the eastern Asian sect. PIERIDOPSIS. Quite variable in stature, pubescence, leaf size and shape, and inflorescence structure, it has been divided into numerous intergrading varieties (see, for example, Fernald, 1941), most of which are actually nothing more than extremes in the total pattern of variation. However, the populations of the Appalachian Mountains and northward can usually be readily differentiated from those of the southeastern Atlantic Coastal Plain from the Dismal Swamp (Virginia) southward, the Gulf Coastal Plain, and adjacent regions (MAPS 10, 11). The Appalachian Mountain and northern populations are here treated as *Lyonia ligustrina* var. *ligustrina,* while those of the southeastern Coastal Plain are considered as *L. ligustrina* var. *foliosiflora.* Variety *ligustrina* can be differentiated from var. *foliosiflora* by its inflorescences that lack leaflike bracts or have only a very few such bracts present, and by its often duller, less coriaceous leaves. In contrast, var. *foliosiflora* has conspicuously leafy inflorescences, and often more coriaceous and lustrous leaves.

Although these two varieties are morphologically distinguishable across wide geographic areas and are essentially geographically isolated, their ranges overlap slightly on the Coastal Plain of southeastern Virginia and the Carolinas, and in small areas of Georgia, northern Alabama, and adjacent parts of Tennessee. In these regions, especially the Carolinas, intermediate plants

can be found that are apparently perfectly fertile. Because these taxa differ in so few characters (and even these are rather difficult to quantify), and because they intergrade freely where they occur sympatrically, they are probably better treated as geographic varieties than as separate species (cf. Pursh, 1814; Elliott, 1817; Nuttall, 1818; and Small, 1903, 1913, 1933).

Michaux (1803) was the first to recognize infraspecific variation in *Lyonia ligustrina*. He recognized two primary varieties ("var. 1. *nudiflora:* racemes nudis" and "var. 2. *foliosiflora:* racemes foliosis"), each of them with two subvarieties. He gave the habitat of var. *nudiflora* as "frigidioribus, per *Etats-Unis,*" and of var. *foliosiflora* as "in sylvis Carolinae inferioris" and "in stagnosis." Michaux was correct in giving the naked inflorescences as the most distinguishing character of var. *ligustrina* (= his var. *nudiflora*) and in recognizing the distinctness of the leafy-bracted plants of the Coastal Plain.

Populations of *Lyonia ligustrina* var. *ligustrina* in the southern Appalachians often show a tendency toward obovate or oblanceolate leaves with acuminate tips. The mountain populations are also often more pubescent. Plants with scattered large bracts in the inflorescences occur in the mountains of western North Carolina, the extreme northwestern portion of South Carolina, and northeastern Georgia.

Lyonia ligustrina var. *foliosiflora* is most variable on the Atlantic Coastal Plain, where two distinctive forms occur. Many plants have nearly glabrous or only sparsely pubescent, narrowly to widely elliptic, obovate or ovate leaves with acuminate apices. These plants tend to be laxly branched and to have large, very prominently leafy inflorescences and reddish twigs. Such plants are common on the Coastal Plain from southeastern Virginia (the Dismal Swamp), south to Florida, and west to Louisiana, eastern Texas, and southeastern Oklahoma. Very similar plants, but usually with larger leaves and less conspicuously leafy inflorescences, occur in the mountains of Arkansas. A few specimens representative of this form are: Virginia, *Fernald & Long 4118* (GH), *14975* (GH); North Carolina, *Randolph 637* (GH); South Carolina, *Little & Wood 14305* (GH), *Godfrey & Tryon 1405* (GH); Georgia, *Wood & Wilson 9351* (GH); Florida, *Curtiss 4718* (GH), *Harbison 17* (GH), *Nash 528* (GH); Mississippi, *Webster & Wilbur 3423* (GH); Arkansas, *Demaree s.n.,* 10-10-1960 (GH), *Palmer 6972* (A), *29205* (A); Louisiana, *Correll 9198* (GH); Oklahoma, *Palmer 21595* (A), *22246* (A).

A second and less common form occurs chiefly in the Carolinas and Georgia and is especially distinct in South Carolina. This form consists of often rather small, rigidly ascending shrubs that have a moderate to dense covering of multicellular hairs and obovate to ± elliptic leaves with mucronate to acute apices. These plants tend to have fewer floral bracts than do plants of the form described above. Extreme individuals have very coriaceous and densely pilose leaves with clearly revolute margins and prominently raised-reticulate veins on their abaxial surfaces. A few specimens characteristic of this form include: North Carolina, *Godfrey 6948* (GH), *48177* (GH); South Carolina, *Godfrey & Tryon 528* (GH), *906* (GH), *1106* (GH); Georgia, *Nuttall s.n.* (GH).

Although the "pubescent" and "glabrous" extremes of *Lyonia ligustrina*

var. *foliosiflora* appear to be quite different, the intergradation is so complete that, in practice, it is impossible to separate the two forms, especially when many collections from the Atlantic Coastal Plain are studied. The morphological extremes are isolated neither ecologically nor geographically and can be found (together with various intermediate plants) in the same localities. For these reasons, all of these plants are considered to be one rather variable taxon.

Michaux (1803) first pointed out the existence of the "pubescent" and "glabrous" extremes of *Lyonia ligustrina* var. *foliosiflora*. He described two unnamed subvarieties of his var. *foliosiflora*, "A. floribus glabellis" and "B. [floribus] subtomentosis." Both Rehder (1924) and Fernald (1941) considered these to be distinct varieties.

The axillary paniculate inflorescences of *Lyonia ligustrina* are produced near the end of the growth of the preceding year, often resulting in a prominent "pseudoterminal cluster." The number of inflorescences in this "cluster" varies from as high as 25 to as low as 1, and a single plant may have a widely varying number of inflorescences clustered at the ends of its branches.

Some confusion has existed concerning the plant to which the Linnaean name *Andromeda paniculata* (1753) refers. Aiton (1799), Willdenow (1799), and Michaux (1803) understood the description of Linnaeus to refer to *Lyonia ligustrina*. Pursh (1814) used *Andromeda paniculata*, and Nuttall (1818) used *Lyonia paniculata*, both in reference to *L. ligustrina* var. *ligustrina*. Others, such as K. Koch (1872) and A. Gray (1878), indicated that the *Andromeda paniculata* of Linnaeus was a different plant. Elliott (1817, p. 490) used *Andromeda ligustrina* for *Lyonia ligustrina* var. *ligustrina* and in the discussion under this taxon added:

> To the accurate and extensive researches of Dr. Muhlenberg, American botanists are indebted for the real history of this plant. It appears to have been the original *Vaccinium ligustrinum* of Linnaeus; it certainly agrees with the Linnaean description of that plant as far as it extends. Modern botanists have viewed it as the *Andromeda paniculata* of Linnaeus, but whoever attends to the description of that plant, in the early additions of the Species Plantarum, will readily perceive that its great author must have had a very different one in view.

The views expressed by Elliott seem to be correct. The Linnaean description of *Andromeda paniculata* is quite ambiguous in that some characters seem to be describing a species of *Leucothoë*. The description seems to fit either *L. racemosa* (L.) Gray or *L. recurva* (Buckley) Gray with respect to three characters: "racemes secundis," "corollis sub-cylindricis," and "foliis . . . crenulatis." Yet Linnaeus's description does state that the racemes are naked and paniculate, characters that could be interpreted as referring to *Lyonia ligustrina*. Koch (1872) listed *Andromeda paniculata* L. as a synonym of *Leucothoë racemosa* (L.) A. Gray, which he called *Lyonia racemosa*. A specimen in the Linnaean Herbarium (sheet no. 563.14, microfiche photo seen), labeled *paniculata*, has the letter "K" near the base of the specimen, indicating that it was collected by P. Kalm. The sheet contains a fruiting specimen of *Lyonia ligustrina* var. *ligustrina* and a flowering specimen of

Leucothoë racemosa; this probably explains the confusing description given for *Andromeda paniculata* in the *Species Plantarum* (1753)! The name *Andromeda paniculata* is here lectotypified by the flowering element (i.e., *Leucothoë racemosa*). It should be noted that this same taxon was described by Linnaeus (1753) as *Andromeda racemosa.* The proper name of this species is thus *Leucothoë racemosa.*

Lyonia Nutt. sect. MARIA (DC.) C. E. Wood, Jour. Arnold Arb. **42:** 48. 1961.

Leucothoë D. Don sect. *Maria* DC. Prodr. 7(2): 602. 1839. *Andromeda* L. sect. *Maria* (DC.) Gray, Man. Bot. No. U. S. 266. 1848. *Pieris* D. Don sect. *Maria* (DC.) Bentham & Hooker, Gen. Pl. **2:** 588. 1876. *Andromeda* subsect. *Maria* (DC.) Gray, Synopt. Fl. N. Am. **2**(1): 32. 1878. *Lyonia* Nutt. subg. *Maria* (DC.) Drude in Engler & Prantl, Nat. Pflanzenfam. IV. **1:** 44. 1889. *Neopieris* Britton & Brown, Illus. Fl. ed. 2. **2:** 690. 1913. *Xolisma* Raf. sect. *Maria* (DC.) Rehder, Jour. Arnold Arb. **5:** 55. 1924. TYPE SPECIES: *Lyonia mariana* (L.) D. Don.

Desmothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Lyonia lucida* (Lam.) K. Koch.

Deciduous or evergreen shrubs, usually spreading vegetatively by horizontal underground rhizomes, the branches with homogeneous pith. Indumentum of unicellular hairs and multicellular, biseriate-stalked, mostly short-headed hairs. Buds with 2 to 6 (to 8) imbricate scales. Leaves entire, with unlignified or only slightly lignified epidermis, lacking hypodermis. Flowers usually 5-merous, in fascicles; calyx lobes valvate in bud; corolla cylindrical, or cylindrical with swollen base; filaments with long, unicellular hairs near base or merely roughened, with pair of well-developed spurs below junction with anthers; placentae positioned centrally (to nearly basally) on columella. Capsules with pale, slightly to strongly thickened sutures that usually adhere to an adjacent valve in dehiscence; seeds oblong-ovoid to spindle shaped, ends often truncated.

DISTRIBUTION. Chiefly United States, Coastal Plain from Connecticut south to Florida, west to Oklahoma and eastern Texas; also in Cuba.

NUMBER OF SPECIES (taxa). 2 (2).

7. **Lyonia mariana** (L.) D. Don, Edinburgh New Philos. Jour. **17:** 159. 1834.

Andromeda mariana L. Sp. Pl. 393. 1753. *Andromeda pulchella* Salisb. Prodr. 289. 1796, *nomen superfluum. Leucothoë mariana* (L.) DC. Prodr. **7:** 602. 1839. *Pieris mariana* (L.) Bentham & Hooker, Gen. Pl. **2:** 588. 1876. *Neopieris mariana* (L.) Britton in Britton & Brown, Illus. Fl. ed. 2. **2:** 691. 1913. *Xolisma mariana* (L.) Rehder, Jour. Arnold Arb. **5:** 51. 1924. Type: "habitat in Virginia," *Kalm s.n.* (lectotype, LINN sheet no. 563.5, microfiche photo seen).

Andromeda grandiflora Meerb. Pl. Select. Ic. Pictae, p. [8]. *t. 25.* 1798. TYPE: "Carol. merid," *J. Fraser s.n.* (lectotype, here designated, L!).

Andromeda mariana L. var. *ovata* Veillard in Duhamel, Traité Arbres Arbustes, ed. 2. 177. [1800–]1801–1819 (but this description probably

published ca. 1803). TYPE: (not seen).

Andromeda mariana L. var. *oblonga* Veillard in Duhamel, Traité Arbres Arbustes, ed. 2. 177. ca. 1803. TYPE: (not seen).

Andromeda mariana L. var. *latifolia* Pers. Synopsis Pl. **1:** 481. 1805. TYPE: (not seen).

Andromeda mariana L. var. *ovalis* Sims, Curtis's Bot. Mag. **38:** *t. 1579.* 1813. TYPE: (not seen).

Andromeda mariana L. var. *angustifolia* Pursh, Fl. Am. Sept. **1:** 294. 1814. *Leucothoë mariana* (L.) DC. var. *angustifolia* (Pursh) DC. Prodr. **7:** 602. 1839. TYPE: (not seen).

Xolisma mariana (L.) Rehder f. *vestita* Rehder, Jour. Arnold Arb. **5:** 51. 1924. *Lyonia mariana* (L.) D. Don f. *vestita* (Rehder) Parks, First Sci. Field Meet. Palmetto State Park, Texas, 9. 1936. TYPE: United States, Texas, Hardin Co., sandy pine lands, Silsbee, 25 April 1916, *Palmer 9561* (holotype, A!).

Erect deciduous shrub to ca. 1.5 meters tall, with brownish to gray, shallowly and longitudinally furrowed bark, spreading vegetatively by horizontal underground rhizomes. Twigs terete to slightly ridged, slender, with few short-headed hairs, otherwise glabrous to moderately pubescent. Buds ± conical to ovoid, 1–2.5 by 0.9–2 mm., with 2 to 6 (to 8) imbricate bud scales (depending upon age). Leaf blades narrowly to widely elliptic, ovate, or obovate, (2.5–)3–8(–10.5) by 1–4(–5) cm., ± flat, chartaceous to slightly coriaceous, ca. 0.15–0.4 mm. thick; apex acute to rounded-mucronate or very slightly acuminate; base narrowly cuneate to rounded; margin entire, plane to slightly revolute; venation brochidodromous to eucamptodromous, with 3° veins reticulate to percurrent; adaxial surface with sparse short-headed hairs, often otherwise glabrescent, the midvein, especially proximal portion, with sparse to dense pubescence that sometimes extends to 2° (or even 3°) veins, the 3° and higher order veins slightly visible to obscure, the 2° veins not depressed; abaxial surface with sparse short-headed hairs, otherwise glabrous to densely pubescent on midvein and often also on 2°, 3°, or even higher order veins, the 3° and higher order veins slightly visible to obscure, the 2° veins slightly raised and visible, sinuous, irregular or smoothly arching, curving toward apex; petiole (1.5–)2–7.5 mm. long, with short-headed hairs, otherwise sparsely to densely pubescent adaxially or all around. Flower buds above vegetative buds; inflorescences fasciculate, to 15-flowered. Pedicels slender to moderately stout, 5–19 mm. long, with short-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to ovate, 0.8–2 mm. long, often persistent; bracts to ca. 4.5 mm. long, similar to bracteoles in shape, deciduous. Flowers usually 5-merous; calyx lobes elongate-triangular to linear, with acute to acuminate apices, often slightly swollen at base, 3–9.5 by 1–4 mm., valvate, both surfaces with scattered short-headed hairs, otherwise glabrous to densely pubescent, deciduous in fruit; corolla cylindrical, 7–14 by 4.5–9 mm., white or rarely pink, abaxially with very sparse short-headed hairs, often appearing glabrous; filaments almost completely covered with long-unicellular hairs, 4–7 mm. long, with 2 usually well-developed spurs below anther-filament junction, anthers 1.5–3 mm. long; ovary glabrous or occasionally very sparsely pubescent, placentae central to nearly basal. Capsule

ovoid with constricted and truncated apex, 4–6.5 by 3–6 mm., with very sparse short-headed hairs, otherwise glabrous or very sparsely pubescent, with pale, moderately to strongly thickened sutures that in dehiscence usually remain attached to an adjacent valve (but sometimes with age separate as unit from both valves); seeds 0.7–1.5 mm. long. (FIGURE 29; see also Meerburg (1798), Duhamel (1803), Sims (1813), Britton & Brown (1913), Harshberger (1916), Gleason (1952), Graves (1952), Grimm (1957), Vines (1960), Wood (1961), Radford, Ahles, & Bell (1968).)

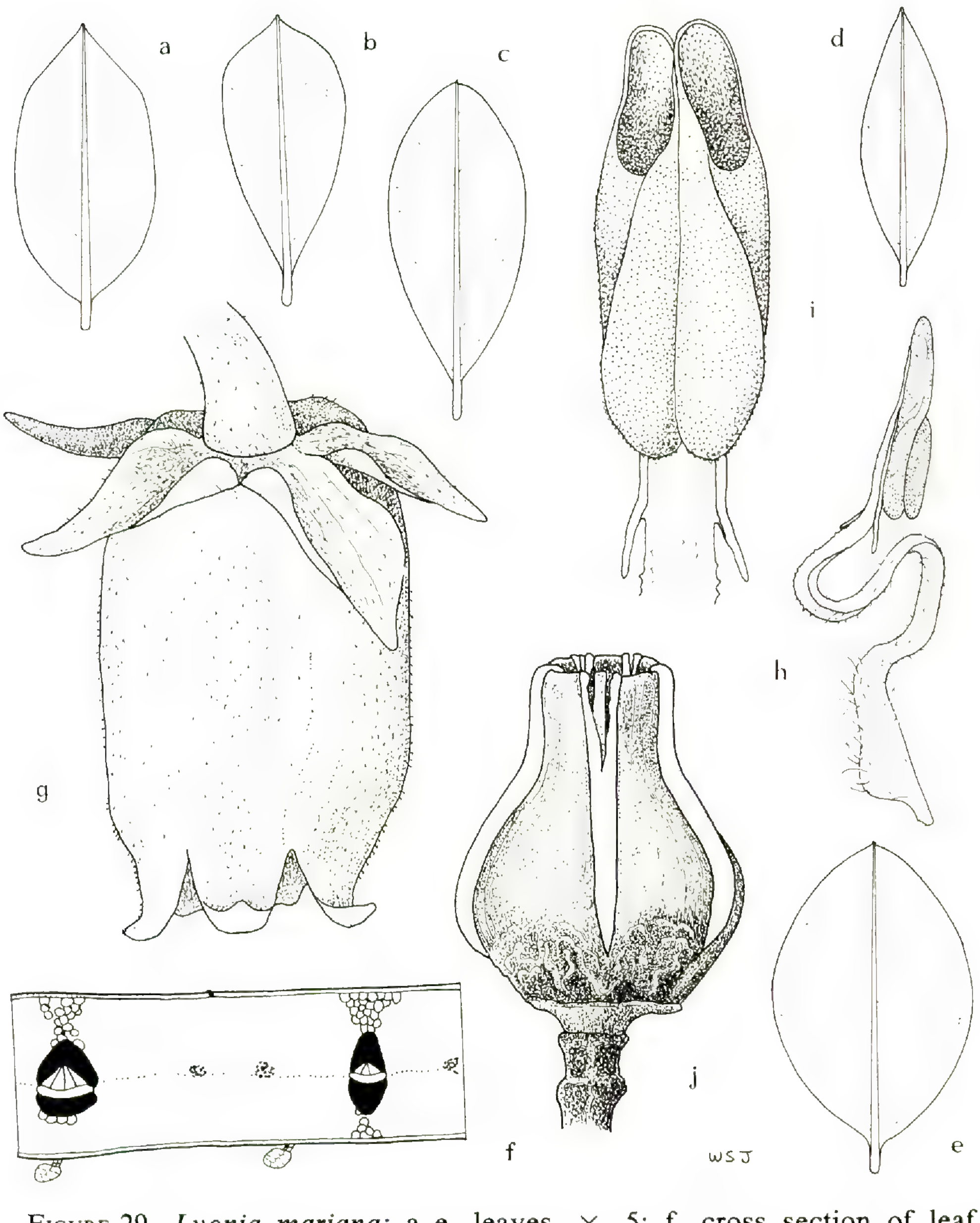
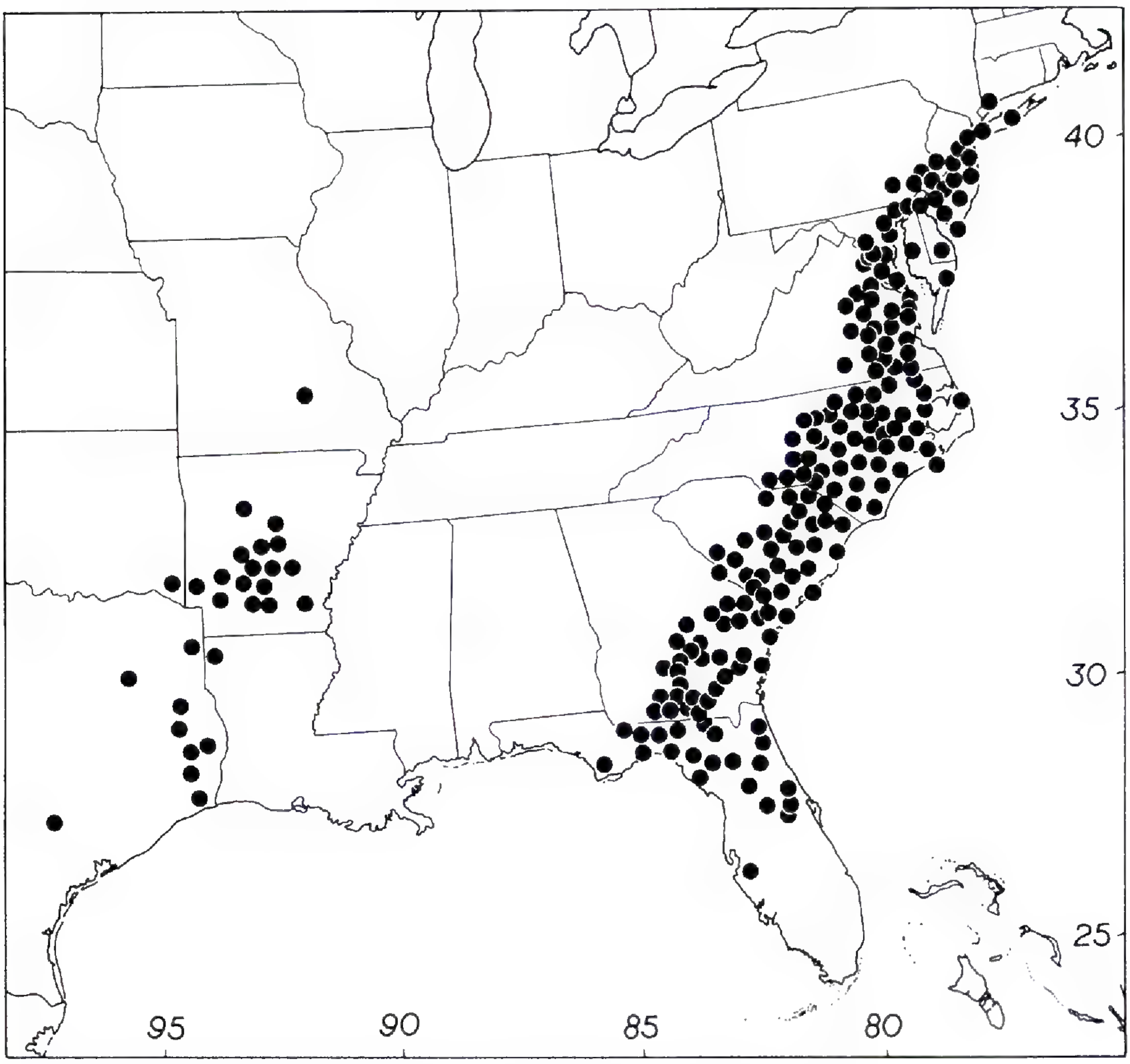


FIGURE 29. *Lyonia mariana:* a–e, leaves, × .5; f, cross section of leaf blade, × 50; g, flower, × 6; h, stamen, × 12.5; i, anther, adaxial surface, × 25; j, capsule, × 6.

DISTRIBUTION AND ECOLOGY. United States, chiefly Atlantic Coastal Plain from Connecticut and Long Island (New York) to Florida, with disjunct populations in eastern Texas, Louisiana, Arkansas, southeastern Oklahoma, and Missouri (MAP 12). Sunny habitats, forest margins, roadsides and railroad grades, shrub bogs, open *Pinus* and/or *Quercus* woods, thickets, old pastures, *Pinus rigida* barrens, *Pinus-Serenoa* flatwoods, grassy savannas, deciduous swamps (esp. of *Acer* or *Liquidambar*), pond margins, sheltered portions of coastal dunes. Flowering chiefly late April to early June.

COMMON NAMES. Stagger-bush, wicks.

REPRESENTATIVE SPECIMENS. **United States.** CONNECTICUT. Fairfield Co.: Stratford, *Coles s.n.*, July 1903 (CONN). NEW YORK. Nassau Co.: E. Williston, Long Island, *Churchill s.n.*, 28 Sept. 1899 (GH). Richmond Co.: N. shore, *Drushel 6385* (US). Suffolk Co.: Ocean Beach, *Lighthipe s.n.*, Sept. 1913 (TEX). NEW JERSEY. Burlington Co.: Atsion, along Mullica R., *Churchill s.n.*, 15 June 1946 (MSC). Cape May Co.: Bennett Bog, 3.6 mi. N. of Cape May, *Crow 109* (MSC). Cumberland Co.: 2 mi. E. of Milville, *Lems 60.05.25.02* (MSC).



MAP 12. Distribution of *Lyonia mariana*.

Mercer Co.: N. of Maple Shade, *Long 53191* (GH). Monmouth Co.: near Asbury Park, *Van Sickle s.n.*, 12 July 1894 (US). PENNSYLVANIA. Chester Co.: Nottingham Barrens, *Pennell 1430* (US). Montgomery Co.: Willow Grove, *Wismer 69* (GH). DELAWARE. New Castle Co.: W. of Vandyke, *Tidestrom 11895* (GH). Sussex Co.: 0.8 mi. N. of Fenwick, *Judd 29* (MSC). MARYLAND. Anne Arundel Co.: Bodkin Creek, *Smith s.n.*, 1 June 1876 (US). Cecil Co.: Elks Neck, *Leonard 5993* (US). St. Marys Co.: 2 mi. W. of Clements, *Smith 5427* (US). Worcester Co.: near Snow Hill, *Gleason s.n.*, 6 June 1934 (DUKE). DISTRICT OF COLUMBIA: Swamp near Reform School, *McCarthy s.n.*, June 1885 (US). VIRGINIA. Caroline Co.: at Mattaponi R. off Co. Rd. 722, *James 13811* (NCU). Chesterfield Co.: E. of jct. of Co. Rd. 619 and U.S. 95, *James 5067* (NCU). Gloucester Co.: 3 mi. NW. of Gloucester Point, *Harvill 12440* (NCU). Louisa Co.: 1.5 mi. W. of jct. of Va. 22 and U.S. 522, *James 13832* (NCU). Lunenburg Co.: S. of Kenbridge, *James 3053* (NCU). Nansemond Co.: S. of South Quay, *Harvill 13828* (NCU). New Kent Co.: 1.4 mi. S. of jct. of Co. Rds. 637 and 1002, *Gillespie 624b* (NCU). NORTH CAROLINA. Beaufort Co.: 3 mi. S. of Chocowinity, *Radford 33395* (NCU). Brunswick Co.: 13 mi. NW. of Supply, *Wilbur 5533* (DUKE). Edgecombe Co.: 0.5 mi. S. of Speed, *Radford 36852* (NCU). Gates Co.: White Oak Pocosin, *Duke 780* (NCU). Onslow Co.: 1 mi. E. of Catherine Lake toward Chinquapin, *Wilbur 4081* (FSU). Orange Co.: 0.5 mi. E. of jct. of N.C. 87 and Route 1727, *Whigham 1992* (NCU). Randolph Co.: 4.4 mi. SE. of Liberty, *Bell 12037* (NCU). Sampson Co.: 2.8 mi. NNW. of Widway, *Ahles 24599* (NCU). Union Co.: 2 mi. WSW. of Marshville, *Ahles 27586* (NCU). SOUTH CAROLINA. Beaufort Co.: 1.1 mi. N. of Pritchardville, *Ahles 12374* (NCU). Berkeley Co.: 1.6 mi. S. of Wadboo Creek, *Bozeman 9145A* (NCU). Georgetown Co.: 5.5 mi. S. of Georgetown, *Godfrey & Tryon 199* (DUKE). Lancaster Co.: 0.4 mi. NNW. of Little Lynches Creek near U.S. 601, *Ahles 27435* (NCU). Lexington Co.: 3.5 mi. NE. of Gaston, *Radford 23379* (NCU). Marion Co.: S. of Britton Neck by Road 49, *Bell 7866* (NCU). GEORGIA. Appling Co.: 3 mi. SW. of Baxley, *Duncan 10925* (DUKE, MO, TEX). Effingham Co.: S. of Stillwell, *Bozeman 4108* (NCU). Laurens Co.: ca. 25 mi. S. of Dublin toward McRae, *Wilbur 3032* (FSU). Lowndes Co.: 10 mi. N. of Valdosta, *Faircloth 3739* (MO, NCU). Screven Co.: 3.5 mi. N. of Newington, *Kral 24024* (DUKE). Thomas Co.: N. of Thomasville, *Bozeman 4958* (NCU). Turner Co.: 3.7 mi. ENE. of Ashburn, *Faircloth 4353* (NCU). Ware Co.: near Suwannee Lake, *Harper 868* (NCU). FLORIDA. Duval Co.: near Jacksonville, *Curtiss 4717* (US). Lake Co.: Ocala Natl. Forest, SE. of Lake Dorr, *Ray 9835* (NCU). Manatee Co.: Palma Sola, *Tracy 6954* (MO, MSC). Marion Co.: Ocala Natl. Forest, *Mather M-142* (GA). Taylor Co.: 4 mi. N. of Perry, *McDaniel & Godfrey 4312* (FSU, NCU). Volusia Co.: 1.5 mi. E. of Astor bridge, *Kral 6566* (FSU). Wakulla Co.: near Wakulla, *Moldenke 1121a* (DUKE). MISSOURI. Dent Co.: 2 mi. S. of Lake Spring, T. 35 W., R. 7 W., sects. 15, 16, *Kucera s.n.*, 11 May 1953 (GA). ARKANSAS. Clark Co.: 2 mi. S. of Hot Springs–Clark Co. line, *Tucker 6889* (NCU). Drew Co.: near Monticello, *Demaree 14978* (MO, WIS). Faulkner Co.: Cove Creek, *Buchholz 979* (TEX, WIS). Grant Co.: near Poyen, *Demaree 11050* (GA). Pope Co.: Crow Mt., *Tucker 7214* (NCU). Saline Co.: near Bauxite, *Demaree 53814* (VDB). Sevier Co.: near Horatio, *Brinkley 169* (TEX). LOUISIANA. Caddo Co.: 4.5 mi. NW. of Vivian, *Thieret 32265* (DUKE, FSU). OKLAHOMA. McCurtain Co.: 2.7 mi. N. of Tom, *Waterfall 13002* (US). TEXAS. Gonzales Co.: Palmetto State Park, *Reis 106* (DUKE). Hardin Co.: Silsbee, *Correll 29392* (ENCB, FSU, GH, NCU, TEX, US). Henderson Co.: 11 mi. SW. of Athens, Spring Lake, *Correll 29612* (FSU, GH). Jasper Co.: 23 mi. NW. of

Jasper, *Cory 22229* (A). Marion Co.: near Jefferson, *Biltmore Herb. 25g* (US). Tyler Co.: 2 mi. S. of Warren, *Correll 35830* (ENCB, FSU, GH, NCU).

Lyonia mariana is a very distinctive deciduous species that can be recognized immediately by its entire-margined leaves covered with multicellular, short-headed hairs; its flowers borne in fascicles along the upper portions of leafless branches of the previous year; its large, white, more or less cylindrical corollas; its elongated, deciduous calyx lobes; and its peculiar, urn-shaped capsules. It is most closely related to *L. lucida*.

The western populations (see MAP 12) tend to be much more pubescent than those of the Atlantic Coastal Plain, and the most densely pubescent plants of the western region have been described as *Lyonia mariana* f. *vestita* (Rehder, 1924). The branchlets, calyx, and leaves of this form have a moderate to dense covering of long, soft, unicellular hairs; however, there are western plants that are only sparsely pubescent, and some eastern plants that are densely covered with unicellular hairs on the major veins of the leaves. In all other characters the plants of these two regions are identical.

The extensive network of underground rhizomes present in *Lyonia mariana* adapts it well to surviving fires. Many vigorous shoots have been observed growing around charred older branches where the plants had evidently been burned the previous year (pers. obs.).

Lyonia mariana has not been collected in Connecticut since 1903 and is probably extinct there, since the area in which it grew has become increasingly urbanized. Thus, Long Island is probably the present northern limit of its range. The species is also rare in Missouri (occurring only in Dent Co.) and Oklahoma (only in McCurtain Co.).

8. **Lyonia lucida** (Lam.) K. Koch, Dendr. **2:** 118. 1872.

Andromeda lucida Lam. Encycl. 157. 1783. *Desmothamnus lucidus* (Lam.) Small, N. Am. Fl. **29**(1): 64. 1914. *Pieris lucida* (Lam.) Rehder, Mitt. Deutsch Dendrol. Ges. **24:** 266. 1915, non *Pieris lucida* Lévl. Bull. Soc. Bot. France **6:** 207. 1906. *Xolisma lucida* (Lam.) Rehder, Jour. Arnold Arb. **5:** 50. 1924. LECTOTYPE: P-LA (IDC 6207. 404: III. 2!).

Andromeda nitida Bartram ex Marsh. Arbust. Am. 8. 1785. *Pieris nitida* (Bartram ex Marsh.) Bentham & Hooker, Gen. Pl. **2:** 588. 1876. *Lyonia nitida* (Bartram ex Marsh.) Fern. Rhodora **10:** 53. 1908. *Neopieris nitida* (Bartram ex Marsh.) Britton in Britton & Brown, Illus. Fl. ed. 2. **2:** 690. 1913. *Desmothamnus nitidus* Small, Shrubs Florida, 96. 1913. TYPE: "grows naturally in Carolina and Florida" (BM?, not seen).

Andromeda coriacea Aiton, Hortus Kew. **2:** 79. 1789. *Andromeda myrtifolia* Salisb. Prodr. 290. 1796, *nomen superfluum*. *Leucothoë coriacea* (Aiton) DC. Prodr. **7:** 602. 1839. TYPE: "Nat. of North Am., Mr. John Cree" (BM?, not seen).

Andromeda marginata Veillard in Duhamel, Traité Arbres Arbustes, ed. 2 (Nouv. Duhamel). 188. [1800–]1801–1819 (this description probably published in 1803). *Lyonia marginata* (Veillard) D. Don, Edinburgh New Philos. Jour. **17:** 159. 1834. *Leucothoë marginata* (Veillard) Spach, Hist. Veg. **9:** 482. 1840. TYPE: "La Caroline et la Floride" (not seen).

Andromeda nitida Bartram ex Marsh. var. *rhombifolia* Wood, Class Book, ed. 1861. 488. 1861. TYPE: (not seen).

Andromeda lacustris C. Wright in Sauvage, Anal. Acad. Ci. Habana **6:** 250. 1870. TYPE: Cuba, en "tembladeras" de lagunas cerca de Pinar del Río dentro de los pinales, *C. Wright 3664* (holotype, US!; isotypes, GH!, NY (3 sheets)!, P!).

Andromeda coriacea Aiton var. *rubra* Lodd. Bot. Cab. **7:** 672. 1822. *Lyonia marginata* (Veillard) D. Don var. *rubra* (Lodd.) Loudon, Arb. Frut. Brit. **2:** 1110. *fig. 901.* 1838. *Pieris nitida* (Bartram ex Marsh.) Bentham & Hooker var. *rubra* (Lodd.) Rehder in Bailey, Cycl. Am. Hort. **5:** 2622. 1916. *Xolisma lucida* (Lam.) Rehder var. *rubra* (Lodd.) Rehder, Man. Cult. Trees Shrubs, 712. 1927. *Lyonia lucida* (Lam.) K. Koch f. *rubra* (Lodd.) Rehder, Jour. Arnold Arb. **20:** 425. 1935. TYPE: "Carolina and Georgia, growing in sandy forests" (not seen).

Small to moderate-sized evergreen shrub to 2.5(–5) meters tall, with brownish to gray, shallowly and longitudinally furrowed bark, usually spreading vegetatively by horizontal underground rhizomes. Twigs usually sharply 3-angled, slender, erect to arching, with few short-headed hairs, otherwise glabrous to moderately pubescent. Buds ovoid, 1–3 by 0.7–1.5 mm., with 2 to 6 imbricate bud scales (depending upon age). Leaf blades narrowly to widely elliptic, obovate, or slightly ovate, 1–8.5(–10.5) by 0.5–4.5(–5.5) cm., sometimes quite reduced in size toward branch apices, ± flat, quite coriaceous, ca. 0.2–0.45 mm. thick; apex acuminate to acute or rarely rounded; base attenuate or cuneate to rounded; margin entire, usually revolute; venation modified brochidodromous, 3° veins ± reticulate; adaxial surface sparsely covered with short-headed hairs, otherwise ± glabrescent, sometimes sparsely pubescent on proximal portion of midvein, 2° and 3° veins usually obscure to slightly raised and visible; abaxial surface with sparse short-headed hairs, otherwise glabrous, the 3° and higher order veins usually obscure, the 2° veins slightly raised and visible, extending straight (or by slightly arching path) toward margin where they join to form intramarginal vein; petiole 1–8 mm. long, with short-headed hairs, otherwise glabrous or pubescent adaxially; vascular bundle unifacial or occasionally slightly bifacial. Flower buds above vegetative buds; inflorescences fasciculate, to 10- (to 15-)flowered. Pedicels slender to stout, 2.5–13 mm. long, with short-headed hairs, otherwise glabrous to densely pubescent; bracteoles opposite, basal, triangular to ovate, 1–2.5 by ca. 1.5 mm., often persistent; bracts to ca. 4 mm. long, similar to bracteoles in shape. Flowers 5-merous; calyx lobes persistent, elongate-triangular, usually with acute apices, 2–7.5 by 1–2 mm., usually swollen at base; the adaxial side very sparsely to moderately pubescent, the abaxial side with scattered short-headed hairs, otherwise glabrous to moderately pubescent; corolla usually cylindrical with swollen base (often appearing merely cylindrical after drying), 5–9 by 2.5–5 mm., pink, less commonly white or red, abaxially with very sparse short-headed hairs, often appearing glabrous; filaments roughened, 3–5 mm. long, with 2 usually well developed spurs below anther-filament junction, anthers 0.8–1.5 mm. long; ovary glabrous or with few short-headed hairs, placentae central to nearly basal. Capsule ovoid to ovoid-globose, occasionally slightly urn-shaped, 3–5 by 3–5 mm., glabrous or with very few short-headed hairs, with pale, slightly to strongly thickened

sutures that usually remain attached to an adjacent valve in dehiscence; seeds 0.7–1.3 mm. long. (FIGURE 30; see also Duhamel (1803), Curtis (1808), Loddiges (1822), Britton & Brown (1913), Small (1927, 1933), Brown (1945), Gleason (1952), Vines (1960), Wood (1961), Radford, Ahles, & Bell (1968).)

DISTRIBUTION. United States, chiefly Coastal Plain from southeastern Virginia (the Dismal Swamp) to Florida, west to Louisiana, also in Cuba (Pinar del

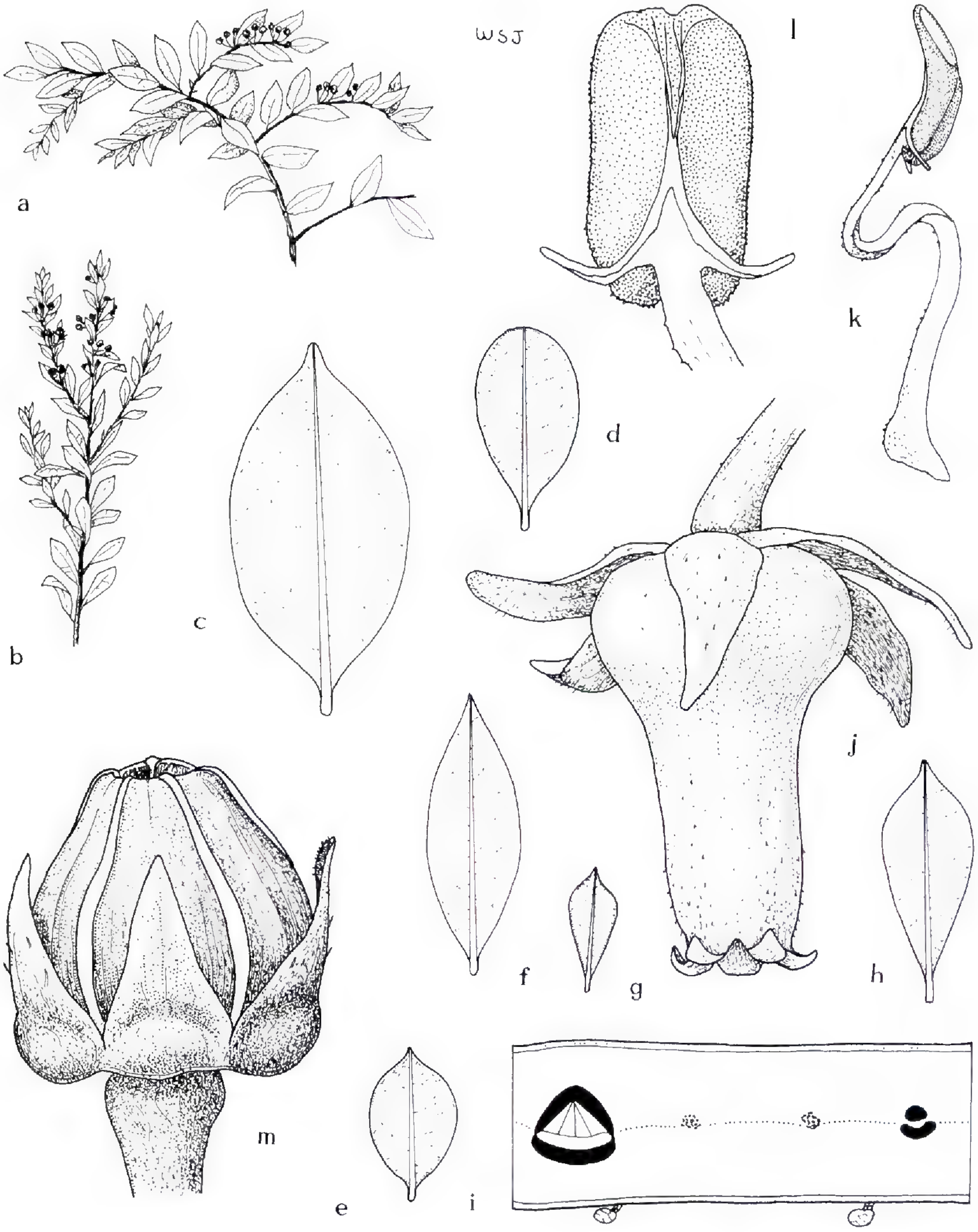
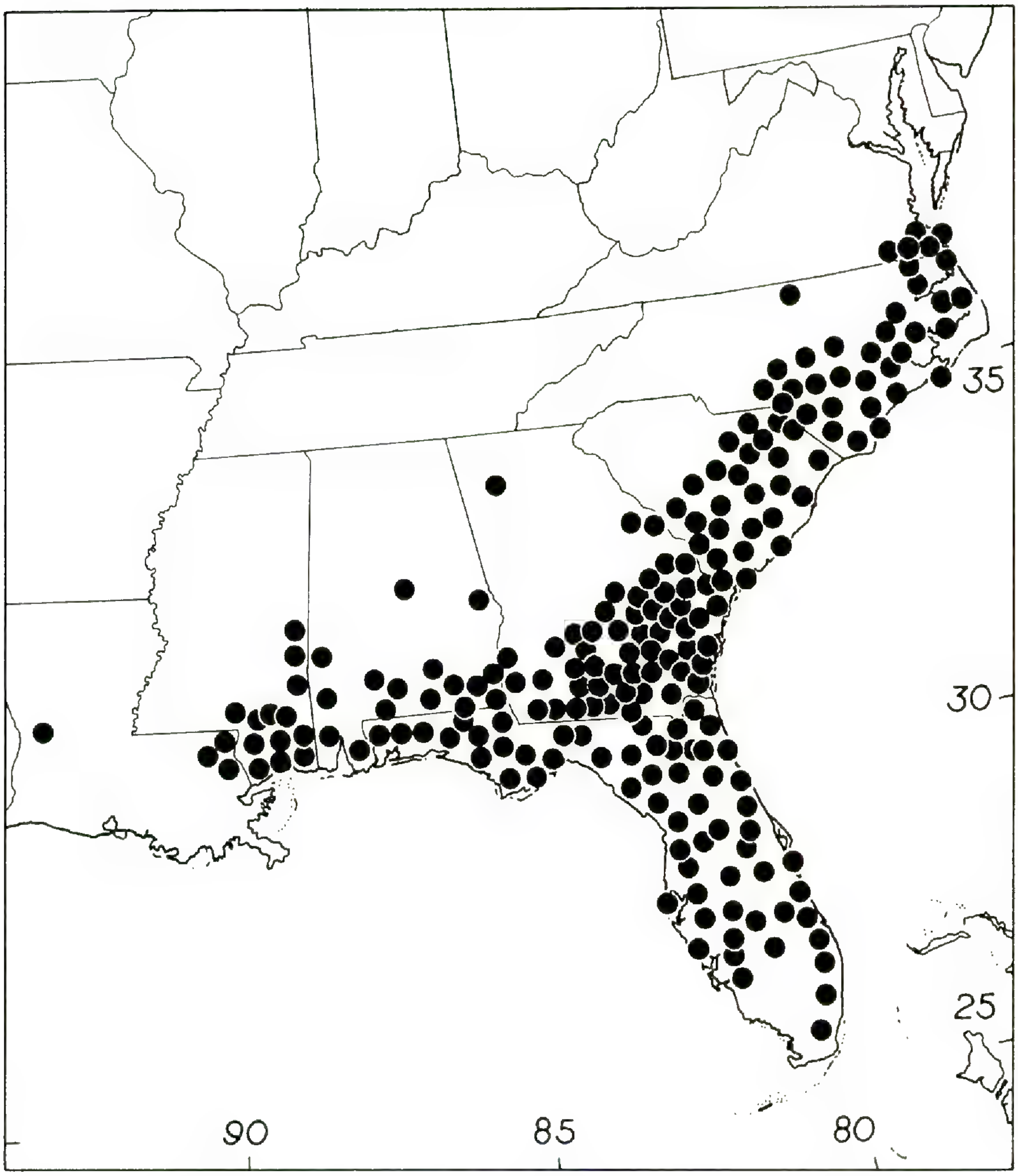


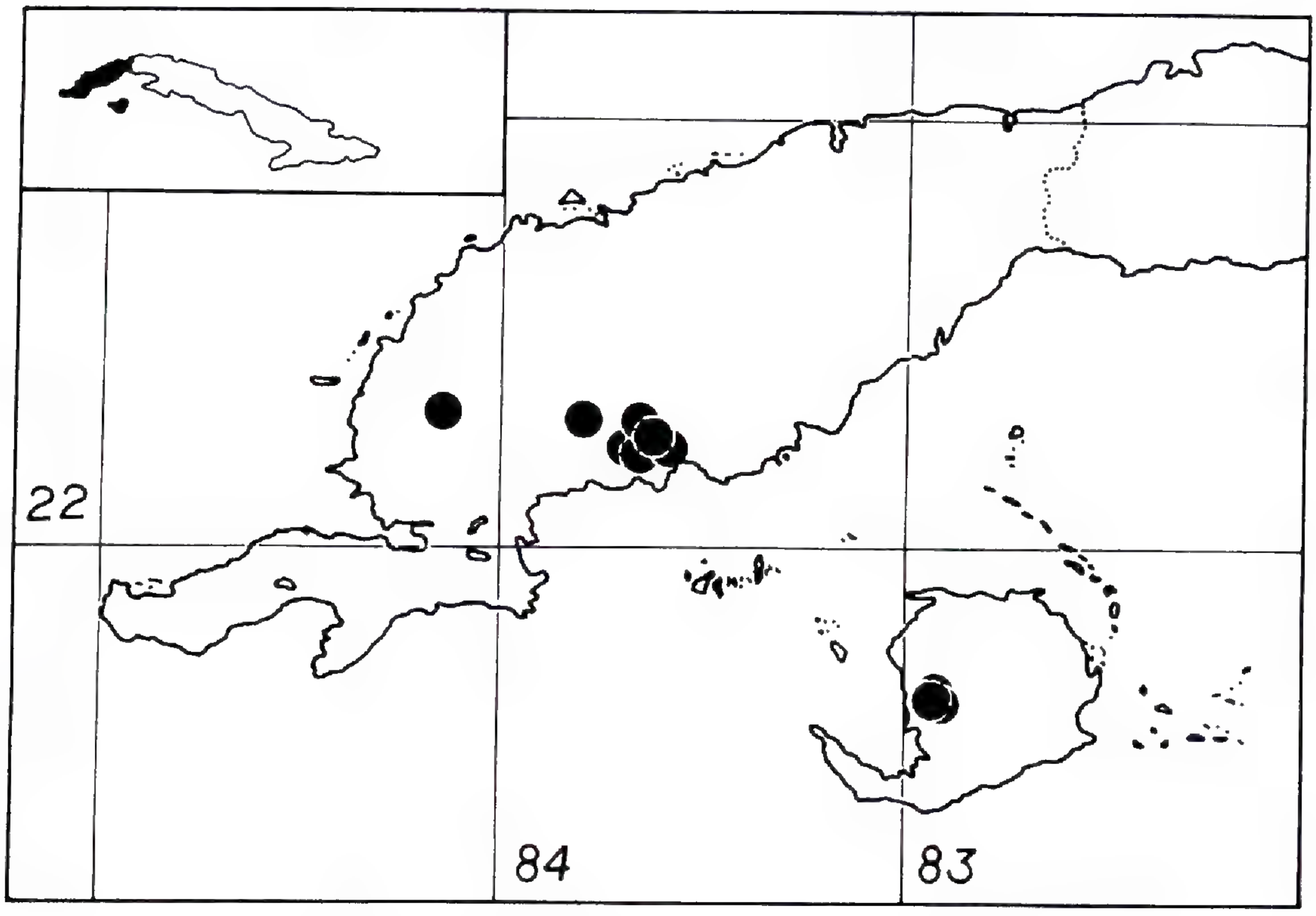
FIGURE 30. *Lyonia lucida:* a, habit in moist, shaded site; b, habit in dry, sunny site; c–h, leaves, × .5; i, cross section of leaf blade, × 50; j, flower, × 6; k, stamen, × 12.5; l, anther, × 25; m, capsule, × 6.



MAP 13. Distribution of *Lyonia lucida* in the United States.

Río prov., Isle of Pines) (MAPS 13, 14). Some interesting disjunct populations around several small ponds in Bartow Co., Georgia (see Greear, 1967).

ECOLOGY. In southeastern U.S., in *Taxodium* swamps, especially around margins, or at base of cypress trees (pers. obs.; see also Coker (1912, esp. *pl. 12,* photograph of dead *Taxodium* with dense collar of *Lyonia* and other shrubs surrounding it at water level) and Lemon (1945)). Very common in many broadleaved swamps; often dominant in moist *Pinus* savannas, shrub-bogs (pocosins), *Pinus-Serenoa* flatwoods, sand scrub and thickets, moist *Pinus* and/or *Quercus* forests, and swamp or pond margins. In Cuba, chiefly in white-sand *Pinus* savannas and near pond margins (Jennings, 1917; Marie-



MAP 14. Distribution of *Lyonia lucida* in Cuba.

Victorin & León, 1944; Seifriz, 1943; Alain, 1946b; Smith, 1954). Flowering mainly late March to early May in southeastern U.S.; chiefly November and December in Cuba.

COMMON NAMES. Fetter-bush, stagger-bush, hurrah-bush (U.S.); clavellina (Cuba).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA. Isle of Wight Co.: S. of Zuni, *Harvill 12043* (NCU). Nansemond Co.: 1 mi. SE. of Blackwater R. on Va. 189, then 2.5 mi. S., *Ahles 58125* (NCU). Southampton Co.: 7 mi. S. of Franklin, *Harvill 13950* (NCU). Virginia Beach: N. of Blackwater R., *Fernald & Long 4116* (GH). NORTH CAROLINA. Beaufort Co.: 3 mi. S. of Chocowinity, *Radford 33404* (NCU). Brunswick Co.: 12 mi. NW. of Supply, *Wilbur 10739* (DUKE). Currituck Co.: Grandy, on U.S. 158, *Ahles 40151* (NCU). Johnston Co.: 2 mi. S. of Parker's Hill, *Radford 27832* (NCU). Onslow Co.: W. of Jacksonville, *Ahles 24076* (NCU). Richmond Co.: Solomon Creek, *J. L. H. s.n.*, 13 Nov. 1917 (NCU). Sampson Co.: 1 mi. NE. of Midway, *Ahles 24608* (NCU). SOUTH CAROLINA. Aiken Co.: 3 mi. NW. of Beech Is., *Radford 9251* (NCU). Berkeley Co.: 5.3 mi. SSE. of jct. of U.S. 176 and S.C. 27, *Ahles 22383* (NCU). Chesterfield Co.: 7.7 mi. N. of McBee, *Radford 13432* (NCU). Horry Co.: Myrtle Beach, *Christenberry s.n.*, 14 July 1938 (NCU). Jasper Co.: 5.5 WNW. of Tillman, *Leonard 1267* (FSU). Richland Co.: along S.C. 12, 1.9 mi. SW. of Kershaw Co. line, *Duke 1614* (NCU). GEORGIA. Bartow Co.: 4.5 mi. SE. of Adairsville, near Quicksand Pond, *Greear 6315* (NCU). Brooks Co.: 3 mi. E. of Quitman, *Bozeman 4899* (NCU). Camden Co.: S. end of Cumberland Is., *Judd 1723* (A, FLAS). Clay Co.: Ft. Gaines, *Wiggington s.n.*,

27 Dec. 1952 (GA). Jeff Davis Co.: 7 mi. SW. of Hazelhurst, *Wilbur 3198* (GH). Lee Co.: near Smithville, *Oosting 78* (DUKE). Liberty Co.: 11 mi. E. of Taylor Creek, *Duncan 2237* (GA). Tattnall Co.: 1.9 mi. NW. of Reidsville, *Ahles 54258A* (NCU). Ware Co.: 10 mi. SW. of Waycross, *Murphy 2410* (NCU). FLORIDA. Bay Co.: St. Andrew State Park, *Wooten 209* (FSU). Duval Co.: 1 mi. S. of Mayport, *Godfrey 61201* (FSU). Dade Co.: W. of Fulford, *Moldenke 454* (DUKE). Lee Co.: Alva, *Hitchcock 191* (US). Leon Co.: Silver Lake Recr. Area, *Lems s.n.*, 8, 10, 11 July 1959 (MSC). Levy Co.: about 5 mi. NE. of Cedar Key, *Godfrey 52824* (FSU, NCU). Polk Co.: near Lake Wales, *Demaree 49452* (FSU, NCU). Union Co.: near Olustec Creek and Road 28, *West & Arnold,* 22 May 1942 (FLAS). Volusia Co.: Tomoka Game Preserve along tributary to Little Tomoka R., *Prichard 968* (FSU). Walton Co.: about 4 mi. W. of Paxton, *Godfrey 61257a* (FSU). ALABAMA. Baldwin Co.: 2 mi. SW. of Theodore, *Iltis et al. 21590* (ENCB, NCU, WIS). Chilton Co.: 6.3 mi. NE. of Clanton, *Clark 17636* (NCU). Covington Co.: 6 mi. NW. of Red Level, *Clark 14422* (NCU). Henry Co.: near Abbieville, *Harbison 4101* (NCU). Lee Co.: Auburn, *Earle & Baker s.n.*, 8 July 1897 (NCU). Mobile Co.: 1 mi. N. of Satuma, *Iltis et al. 21410* (NCU, WIS). Washington Co.: along Bassett's Creek, near U.S. 43 bridge, *Clark 8739* (NCU). MISSISSIPPI. Clarke Co.: 7 mi. SE. of Quitman, *Ray 6986* (MISSA). Forrest Co.: 2 mi. NW. of Eatonville, *Ray 7761* (NCU). Hancock Co.: near Bay St. Louis, *Demaree 32974* (DUKE, MISSA, TEX). Harrison Co.: near Mississippi City, *Demaree 35541* (FSU, NCU). Marion Co.: about 2 mi. S. of Sandy Hook, *Ray 7911* (MISSA). LOUISIANA. St. Tammany Co.: about 3 mi. SE. of Abita Springs, *Thieret 26964* (DUKE, FSU). Tangipahoa Co.: 13 mi. E. of Hammond, *Rose-Innes & Warnock 723* (TEX). Vernon Co.: Kisatchie Natl. Forest, *Cooley & Brass 4026* (NCU). **Cuba.** PINAR DEL RÍO: dry Arroyo Mántua, Damují, *Ekman 11036* (NY); Laguna Santa Maria, S. of Río Feo, vicinity of Pinar del Río City, *Ekman 17282* (K, US); Pinar del Río City, at km. 11 on rd. to Coloma, *Ekman 18253* (K, NY, US); near Laguna Redonda, 11 km. S. of Pinar del Río, *Bro. León et al. 17775* (GH); vicinity of Sumidero, *Shafer & Bro. León 13632* (F, MO, NY, US). ISLA DE PINOS: Los Indios, *Bro. Alain & Killip 2216* (GH, US).

Lyonia lucida is a very distinctive species characterized by coriaceous, persistent, entire-margined leaves with an intramarginal vein and scattered, multicellular, more or less short-headed hairs; fasciculate inflorescences; elongated calyx lobes; usually pink, more or less cylindrical corollas with a swollen base; and roughened filaments with two usually well-developed spurs just below the anther-filament junction. It is also unusual in that the vascular tissue of the leaf midrib and petiole is unifacial or nearly so.

Lyonia lucida is most closely related to *L. mariana*. Although *L. lucida* lacks the strikingly urn-shaped capsule (see FIGURES 29, 30) of *L. mariana,* it often does have the slightly constricted capsule apex; both species tend to have more or less central to nearly basal placentae bearing many ovules. The two species can often be seen growing in close proximity, although *L. lucida* is usually found in wetter situations. Hybrids between these species have apparently never been found.

Lyonia lucida is quite variable in leaf size and shape and in habit. In sunny, dry environments it tends to be a dwarf shrub with rigidly ascending branches bearing very small and narrow leaves, while in damp, shaded localities

it is often quite a large shrub with beautifully arching branches and large, more or less elliptic leaves. When a narrow-leaved plant collected in the dry pine-palmetto scrub of southeastern Georgia was transplanted to the moist environment of a greenhouse, it developed large, elliptic leaves, thus indicating that this difference is mainly environmentally controlled.

The Cuban populations often have slightly longer and more densely pubescent calyx lobes than do plants on the Coastal Plain of the southeastern United States, but in all other respects plants of the two regions are identical.

To be concluded

WILLIAM HAMILTON (1783–1856) AND THE PRODROMUS PLANTARUM INDIAE OCCIDENTALIS (1825)

RICHARD A. HOWARD, KRISTIN S. CLAUSEN,
AND WILLIAM T. GILLIS, JR.†

HAMILTON's *Prodromus* was published in the interval between the descriptive work of Olaf Swartz (1788–1806) and Martin Vahl (1798–1807) and Grisebach's *Flora of the British West Indian Islands* (1859–1864). The publication contains descriptions of plants occurring between the Bahama Islands and Guyana, Venezuela, and Colombia, including all of the Greater and Lesser Antilles. Twenty-four new genera were described, of which four (*Phymosia*, *Rhytachne*, *Torulinium*, and *Emmotum*) are currently accepted. Two genera, *Etericius* (Rubiaceae?) and *Cypellium* (Styracaceae?) have not been satisfactorily placed to family in recent botanical studies. Of the 222 species listed, 153 were indicated (by a dagger) as new. Gillis compiled from this volume a list of 15 names that have not been included in *Index Kewensis* or its supplements. Other binomials represent new names or new combinations, which have also not been indexed. Subsequent monographers have found Hamilton's work difficult to use. The binomials have been credited to Hamilton, Desvaux, Desvaux in Hamilton, or Desvaux ex Hamilton. Hamilton collected in the West Indies, studied and described living material, and had access to the herbarium of Desvaux. Hamilton's own collections applicable to the *Prodromus* are said to be in Paris and Charkov, but none has been located (Stafleu, 1963, p. 191). The names of numerous Hamilton species from the Lesser Antilles will remain dubious until collections can be located.

Hamilton usually cited "Herb. Prof. Desv." without indicating a collector. Desvaux's herbarium has been perplexing to subsequent workers. Following Desvaux's death in 1856, his general herbarium was sold by his son to Alphonse Lavallée. Although it was advertised as 40,000 sheets, Bonnet (1907, p. 276, footnote) felt that this was an exaggeration. Lavallée moved the collection to Segrez (Seine-et-Oise). It was given to the Museum of Natural History, Paris, by his widow in 1896 (Bureau, 1896). The collection has been subsequently integrated into the general herbarium. Desvaux did not personally collect botanical specimens beyond the region of Angers. He received specimens from many correspondents, but the collector is not noted and the area stated is rarely specific. De Candolle (1880) noted, "Les omissions ou indications fausses de pays et la similitude de certains échantillons avec ceux du Muséum rendent cet herbier fort curieux." Hamilton's personal collections have not been located in the Desvaux herbarium, although Hamilton mentioned seeing living material and apparently made specimens. The collec-

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tions from Jamaica in the Desvaux herbarium were probably obtained from his father-in-law, Tussac, who had collected in Jamaica. Guyanan material may have been acquired from Richard. Killip (1938) suggested that the type of *Passiflora cyathophora* Ham. was a Richard collection, while the type of *Passiflora gossypifolia* Ham. was from Poiteau.

Recently, Dr. George R. Proctor, with the assistance of Dr. Alicia Lourteig, was able to locate a number of specimens in Paris that had been cited by previous authors. All bear a Museum of Paris label with the notation "Herbier de N. A. Desvaux"; the majority are indicated as gifts of Mme. Vve. Lavallée in 1896. However, the label on a specimen of *Balantium cordifolium* indicates that it was from the herbarium of Adrien de Jussieu, given by his children in 1857. All of the specimens seen to the present bear Desvaux's hand on part of the label, usually with the scientific name followed by "Desvaux" and the reference to Hamilton's *Prodromus*. The specimens are fragments and are rarely more than small bits. Perhaps in time all of the voucher specimens for the names in Hamilton's *Prodromus* will be located in the general herbarium in Paris.

Before his death on June 20, 1979, Dr. Gillis was working toward a new flora of the Bahama Islands. He was awarded a grant from the Penrose Fund of the American Philosophical Society to visit Paris and London to seek out Hamilton specimens. In a report to the American Philosophical Society, he wrote, "Photographs were taken of all specimens that were found. Other specimens of Hamilton, representing the other one hundred eleven names published in the *Prodromus*, were examined and annotated as time permitted" (Gillis, 1979). In a cooperative effort, Howard had compiled a list of the plants of the Lesser Antilles that Gillis was to seek, and a joint publication was planned. Dr. John Beaman kindly located a file on Hamilton in Gillis's office after his death. A brief introduction to a paper was outlined, but the majority of the notes on individual species bear cryptic marks that can not be interpreted. The photographs have not been located. The present paper is an attempt to record what is known of William Hamilton and the specimens basic to the *Prodromus*.

William Hamilton appears to have been a perplexing, misunderstood, and poorly known individual. A brief notice of his death on May 23, 1856, in the Octagon House, Union Street, Plymouth, England, at the age of 73, was published in the *Plymouth, Devonport & Stonehouse Herald* on May 31, 1856. Thus it can be determined that Hamilton was born in 1783, but where and when are not known. He attended the University of Dublin from 1799 to 1805 and received a B.A. degree. He received an M.A. from Oxford University in 1808, and a Bachelor of Medicine degree in 1809. Years later, in an application for a Radcliffe Travelling Fellowship, Hamilton wrote, "Soon after this event, having first published a small Medical Work (now I believe out of print), I went abroad and spent a considerable number of years travelling among the various islands of the West Indies, from whence I transmitted to the late Sir Joseph Banks an Account of the memorable eruption of Morne Agarou, in the island of St. Vincent, which was read before the Royal Society, and honoured as I have reason to believe with a place in their transactions"

(Hamilton, 1832–35). This account has not been located in the published records of the Royal Society. The eruption occurred April 27, 1812.

Hamilton (1832–1835) stated, "During my absence from England I applied with considerable assiduity to the Medical Botany of the different places which I visited, and instituted experiments for the purpose of determining the properties of various Plants, the growth of our Colonies, and ascertaining their applicability to the several purposes of the Arts, Manufactures, Domestic Economy, Commerce or Medicine. . . ."

Hamilton arrived in the West Indies in March, 1810, and "quitted the tropics" in 1817. A full chronology of this period eludes us. We know from comments in articles cited in his bibliography that Hamilton was on Nevis on April 27, 1812, and again in May and June of 1814. In May, June, and July, 1815, he was on Dominica, and in January, 1816, on Guadeloupe. He wrote of being in Haiti in the months of January through July but did not specify the year. He visited "the Danish territories," probably St. Thomas and St. Croix, at unspecified dates; spent a Christmas on Nevis; visited Antigua and Barbados; was a "resident at Scarborough," Tobago, in an October; and spoke of "Puerta d'España" on Trinidad. After he returned to England he stated, "I availed myself of every opportunity to improve my acquaintance with the Botany of Equinoctial America and its Islands, with the double view of arranging the materials I had collected during my travels and preparing myself for a second and more advantageous visit to the same regions . . ." (Hamilton, 1832–1835). In an undated letter (Brit. Mus. (Nat. Hist.) Banks Corresp. 160–162) about 1819, Hamilton wrote to Sir Joseph Banks, "Doctor Hamilton has the honour of submitting to Sir Joseph Banks a specimen of the Flora Occidentalis upon which he is engaged, and will feel much obliged by any advice or information which Sir Joseph may find leisure to give him. . . . Owing to the dearness and rarity of Swartz Flora—a compendium of West Indian Botany must he conceives be an acceptable present to the Visitor to the Antilles—and the only question is how far he can be deemed competent to the task of its completion. Mr. Brown [Robert Brown, librarian for Sir Joseph Banks at this time] perhaps may find leisure amidst his other useful occupations to favour him with a few suggestions—having in mind however that the person who requires them is as yet but a mere novice in the Science. . . ." Hamilton added to this letter a resumé in French of a message he had sent to Baron de Dupuy at Cap Henri (Haiti), asking that living plants of *Krameria* and *Theophrastus* be sent to the Royal Botanical Gardens.

Thus it appears that Hamilton was engaged in preparing a "flora occidentalis" by 1820. As he later indicated (Hamilton, 1832–1835), he applied for a vacancy in the Radcliffe Travelling Fellowship in 1821. Unfortunately, he applied too late—all votes were "pre-engaged." He then went to France, where he "pursued the study of tropical botany, under the auspices of the learned and amiable Mr. Desvaux, professor of Botany at the University of Angers, and with the assistance of his rich and extensive herbarium." His absence from England prevented him from applying for the second vacancy in the Radcliffe fellowship, which occurred in 1822. Why Hamilton chose France

for study rather than a British institution is not known. Throughout his career he appears to have been a *persona non grata* in his own country. "Soon after my return from France," Hamilton wrote, "I prepared and published, as the first fruits of my Botanical Studies, a 'Prodromus Plantarum Indiae Occidentalis,' a small octavo volume, containing the Characters of some New Genera, the Descriptions of some New Species, and the revision of some errors in former works on the same subject. For this little work, which was published by Messrs. Treuttel and Würtz, of Soho-square, in 1825, I was honoured with a Letter of Thanks by the National Institute of France" (Hamilton, 1832–1835).

On July 10, 1830, Hamilton wrote from Plymouth to W. J. Hooker in Glasgow of his plans "to arrange and publish in monthly or quarterly numbers 'til complete, a complete Flora of the West Indies—a work which is undoubtedly a desideratum and an important one in West Indian botany." Neither a publication nor a manuscript of this work has been located. In an article in the *Pharmaceutical Journal* (**5:** 31. 1846), Hamilton referred to his unpublished flora of the Antilles and quoted a "note as I find it entered in my manuscript."

At some time between 1832 and 1835, Hamilton (who then signed himself "William Hamilton M. B. And Corresponding Member of the Medico-Botanical Society of London") applied to His Grace, the Archbishop of Canterbury, and nine other "Electors under the Will of the late Dr. Radcliffe" for the "approaching vacancy in Doctor Radcliffe's Travelling Fellowship." The application was a printed document (Hamilton, 1832–1835) indicating his interest in returning to the tropics and "exploring those interesting regions over which the illustrious Humboldt has shed a classic glory, and treading, although by no means *pari passu,* in his distinguished footsteps." There is no indication whether Hamilton was successful with this application. In 1838 he wrote that he was refused a post as "Stipendiary magistrate" because he wanted to pursue botanical studies in the intervals not occupied by magisterial duties. It was during this period that he was regularly writing letters to the *Gardener's Magazine* regarding plants of the American tropics, and Lanjouw and Stafleu (1957) recorded that Kew received specimens of "medicinal plants" from Hamilton collected between 1829 and 1838.

Hamilton's *Prodromus* was published in October, 1825. William Stearn has noted in the copy in the library of the British Museum (Natural History) that "a copy was presented to the Linnaean Society by the author on 11 Nov. 1825." No contemporary reviews of this work have been located, and later authors have not been kind in their comments. Grisebach (1859–1864, p. vii) stated that Hamilton's *Prodromus* "is a pamphlet on certain new or doubtful species, but which for the most part cannot be identified." In the text of *Flora of the British West Indian Islands,* Grisebach appears to have accepted two species, *Eriochloa punctata* and *Sporobolus purpurascens,* both of which he attributed to Hamilton. An additional six species attributed to Hamilton are cited in synonymy. The genus *Tobinia* (with five species), published by Hamilton, was attributed to Desvaux by Grisebach.

Urban (1898) seemed to indicate that Desvaux sent specimens to Hamilton,

but there is no other confirmation of this. Urban further stated (free translation), "Moreover, some well-known species are to some extent redescribed with unnecessary modifications of the names. Since the diagnoses are usually too brief, or too few in characteristics, with many species also obviously transferred to incorrect genera, and since the originals are accessible to ever fewer botanists, this little work has been a cross and a scandal for all those concerned with West Indian or Guyanan flora. We must consider ourselves fortunate, therefore, that Hamilton did not fulfill his intention to describe all West Indian plants in a larger work." Urban is known to have annotated two specimens and to have corrected the identification of one (*Rhus rufescens* Ham. = **Brunella comocladifolia** Humb. & Bonpl.). Still other names, placed in synonymy in various entries in the *Symbolae Antillanae,* are indicated in the list of equivalents in this paper.

None of the genera named *Hamiltonia* by various authors is named after this William Hamilton. Apparently Desvaux named one specimen *Acacia hamiltonii,* and Hamilton published this in the *Prodromus.* Other taxa described in the *Prodromus* have subsequently been renamed in Hamilton's honor, among them a *Pennisetum* and a *Fimbristylis* by Steudel, an *Ardisia* by A. de Candolle, a *Peperomia* by Miquel, and a *Rhynchospora* by Kunth.

The entries in Hamilton's *Prodromus* are given localities in specific or general areas: 41 from Guyana; 37 from Hispaniola plus 4 from Santo Domingo and 6 from Haiti; 30 from Jamaica; 21 from the Antilles; 17 from Ind. Occ.; 15 from Nevis; 12 from Cayenne; 8 from Puerto Rico; 7 from St. Kitts; 4 from Guadeloupe; 3 each from Cartagena, Martinique, the Bahamas, and Carribeis; 2 each from St. Thomas, Cuba, Caracas, Tobago, and Dominica; and 1 each from the Barbados and Antigua. Most of the specimens are cited as "Herb. Prof. Desv.," although 28 are indicated as living ("V." or "v.v.") or as dried material ("s.v.").

The *Prodromus* was dedicated to N. A. Desvaux, and it was indicated that he at one time participated in the work. In the preface Hamilton stated, if we correctly interpret the difficult Latin, "The new genera now published for the first time in this small book are brought together on purpose: no recently discovered species is described of which I do not have either specimens or drawings, or descriptions personally prepared at the time the plants were observed growing *in situ,* or specimens well-preserved in Prof. Desvaux's herbarium with descriptions and illustrations accurately prepared by him." Elsewhere Hamilton said of Desvaux, "This distinguished gentleman not only made the treasures of his very rich herbarium accessible with absolute freedom but also honoured me with his counsel and help." He noted also that any errors were his own. It is clear that all the taxa described in the *Prodromus* should be attributed to Hamilton alone.

The specimens from many areas where Hamilton did not visit were from the collections assembled by Desvaux. Other taxa from islands that Hamilton did visit may have been described in the field, represented by drawings or possibly by specimens, or studied later when seeds that Hamilton collected or obtained were grown. For some there is no indication that specimens were prepared. *Cyrtopodium elegans,* the plant represented in the tinted

frontispiece, is indicated by Hamilton only as a living plant. Dr. Leslie Garay has informed us, however, that a herbarium specimen does exist in the Paris collections.

In the *Pharmaceutical Journal* Hamilton (1847) wrote, "Nearly thirty years have elapsed since I quitted the happy regions of the tropics, and, in the interval, a variety of other subjects have claimed my attention. My specimens have been almost all lost or mislaid, and only a few scattered notes, the disjecta membra of my former labours, are in existence."

A few of Hamilton's new species appear to have been attempts to validate the previous use of a name in Desfontaines's "Cat. Hort. Paris." since Hamilton cited the name as "sine descr." Occasionally Hamilton indicated ("s.v.") that a specimen of a particular taxon was in the Desvaux herbarium. For some binomials that we have indicated as new names or new combinations, Hamilton may have given the basionym and the country but omitted any indication that he had seen a specimen, suggesting that specimens were not in the Desvaux herbarium.

HAMILTON'S NEW GENERA

In the preface to the *Prodromus* (xiv–xvi), Hamilton listed the essential characteristics of 14 new genera. These can be evaluated as follows:

APATITIA. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 107). Listed as a *nomen rejiciendum* of **Bellucia** Raf. (Stafleu, 1978).

BALANTIUM. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 172). Rejected as a later homonym of *Balantium* Kaulf. (1824) (Dicksoniaceae). Now regarded as a synonym of **Parinari** (Chrysobalanaceae).

CORDIOPSIS. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 421). Generally regarded as a synonym of **Cordia** L.

LOPHIA. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 1003). To be regarded as a synonym of **Alloplectus** Martius, *nomen conservandum.*

NEMUM. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 1157). To be regarded as a synonym of **Scirpus** L.

NEUROCARPON. Previously published by Desvaux (Jour. Bot. Desvaux **1:** 119. 1813).

PARALIA. Credited to Hamilton but considered an orthographic variant of **Paralea** Aublet (Farr *et al.*, 1979, p. 1259).

PHYMOSIA. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 133). Currently accepted.

POARIUM. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 1376). To be regarded as a synonym of **Stemodia** L.

RHYTACHNE. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 1518). Currently accepted.

TOBINIA. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 1765). Currently regarded as a synonym of *Fagara* L. or *Zanthoxylum* L.

TORULINIUM. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 1171). Currently accepted.

XYLADENIUS. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 1825). Currently regarded as a synonym of **Banara** L., which Hamilton (*Prodromus*, p. 43) regarded as a *nomen dubium*.

ZYGIS. Farr *et al.* (1979, p. 1894) cite this name as "(Persoon) Desvaux ex Hamilton." Hamilton did not cite Persoon (Syn. Pl. **2:** 131. 1806), where *Zygis* is briefly described as a sectional or generic name. *Zygis* Ham. is referred to *Satureja* L. or *Micromeria* Bentham.

In the body of the *Prodromus*, Hamilton used other generic names for the first time, giving diagnostic characteristics with or without comparisons to existing genera. These are the following:

ARACHNIMORPHA. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 119). Generally regarded as a synonym of **Rondeletia** L.

CATHARTOCARPUS. A later homonym of **Cathartocarpus** Pers.

COCCOSYPSILUM. Hamilton cited Browne's *Coccocipsilum*, and his name is to be regarded as an orthographic variant of the conserved **Coccocypselum.**

CYPELLIUM. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 479), with the name assigned to the Styracaceae. The binomial *Cypellium nervosum*, based on a plant from Guyana, has not been placed in the genus *Styrax* or otherwise used.

DICHROMA. Although this generic name was not listed in *Index Nominum Genericorum*, it is validly published but is a later homonym of **Dichroma** Cav. (1801) (Scrophulariaceae).

EMMOTUM. Credited to Desvaux ex Hamilton (Farr *et al.*, 1979, p. 610) and currently accepted.

ETERICIUS. Credited to Desvaux in Hamilton (Farr *et al.*, 1979, p. 645). This name has been assigned to the Rubiaceae, but the description of *E. parasiticus* can not be placed in representatives of that family from Guyana.

GONOCARPUS. Farr *et al.* (1979, p. 737) indicate this to be a later homonym of *Gonocarpus* Thunb. = **Haloragis** Forster. They state that the type species, *G. jacquinii*, is illegitimate and should be *Combretum alternifolia* Pers. However, the latter is also an illegitimate name for *Combretum decandrum* Jacq.

MAPROUNIA. Farr *et al.* (1979, p. 1039) credited this name to Hamilton and indicated it to be an orthographic variant of **Maprounea** Aublet.

THYANA. Credited to Hamilton by Farr *et al.* (1979, p. 1757). However, Hamilton proposed a new name for *Thouinia* Poit.

The generic names that Hamilton used in the *Prodromus* are variously credited to Hamilton, Desvaux ex Hamilton, Desvaux in Hamilton, or Desvaux in various indices and publications. In several places in the *Prodromus*,

Hamilton cited the names of Desvaux, Beauvois, Richard, or Aublet in brackets. A few of the generic names thus credited to Desvaux had been published elsewhere at an earlier date, but the majority were used for the first time in this publication. Beauvois is the author of *Zosterospermum*; Aublet is the author of *Perama* and *Maprounea* but is not credited by Hamilton for other generic names that were published in his *Histoire des Plantes de la Guiane française*. Richard is not the original author of *Rhynchospora*. Linnaeus and Swartz, the authors of most of the generic names that Hamilton used, are not mentioned.

HAMILTON'S SPECIES

In the list of modern equivalents that follows, we have given the name that Hamilton published, the page reference in the *Prodromus*, and the data supplied as to country of origin, material in the Desvaux Herbarium, and whether Hamilton saw a dried specimen (s.v.) and/or living material (v.v.). The equivalent is indicated as the correct name in accordance with the current code of nomenclature, followed by reference to a publication where the Hamilton name is cited and/or the modern name is used. Where needed, a comment may be supplied and an indication given (P) that the author refers to a specimen in the herbarium at Paris. The designation (P!) indicates that a specimen was seen by Gillis or Proctor. We have no data to indicate whether this was a collection by Hamilton or by some other person. An asterisk (*) indicates that Hamilton declared this entry to be a new species. We have supplied "comb. nov." or "nom. nov." for other entries to indicate our interpretation of Hamilton's action. "Spec. nov." is used to indicate that Hamilton seems to have been describing a new species although he did not indicate this. Hamilton did not cite authorities for the epithets that were not marked as new species. He may have cited synonyms or references to indicate where he obtained the name. Many names, without synonymy or references, had been published previously, generally by Desvaux or Aublet.

LACISTEMA MYRICOIDES (p. 1). Jamaica; Herb. Desv., s.v. = **Lacistema aggregatum** (Berg.) Rusby; Adams, Fl. Pl. Jamaica, 490. 1972.

*PEPEROMIA ALATA (p. 2). Santo Domingo; Herb. Desv., s.v. = **Peperomia alata** Ruiz & Pavon; León & Alain, Fl. Cuba **2:** 27. 1951.

*PEPEROMIA LUNARIA (p. 2). Herb. Desv., s.v. = **Verhuellia lunaria** (Ham.) C. DC.; Moscoso, Catal. Fl. Doming. 132. 1943.

*PEPEROMIA SIMPLEX (p. 2). Jamaica; Herb. Desv., s.v. = **Peperomia simplex** Ham.; Adams, Fl. Pl. Jamaica, 208. 1972.

*PEPEROMIA SPATULATA (p. 2). Herb. Desv., s.v. (P!) = **Peperomia cordifolia** A. Dietr.; Urban, Symb. Antill. **3:** 228. 1902.

*PEPEROMIA SUAVEOLENS (p. 2). Cuba, v.v.; Herb. Desv., s.v. = **Peperomia galioides** Kunth; Urban, Symb. Antill. **3:** 261. 1902.

*PEPEROMIA HEMIONITIDIFOLIA (p. 2). Santo Domingo; Herb. Desv., s.v. = **Peperomia obtusifolia** (L.) A. Dietr.; Urban, Symb. Antill. **3:** 254. 1902.

*PIPER CELTIDIFOLIUM (p. 2). Antilles; Herb. Desv., s.v. = **Piper amalgo** L.; Yuncker, Bull. Inst. Jamaica Sci. II. 8. 1960.

*PIPER SAURUROIDES (p. 3). Puerto Rico, St. Thomas; Herb. Desv., s.v. = **Piper medium** Jacq.; Yuncker, Piperaceae No. S. Am. **1:** 68. 1960.

*PIPER ALARE (p. 3). Cayenne; Herb. Desv., s.v. (P!) = **Piper marginatum** Jacq.; Urban, Symb. Antill. **3:** 172. 1902.

*PIPER CUSPIDATUM (p. 3). Hispaniola; Herb. Desv., s.v. (P!) = **Piper cuspidatum** Ham.; Urban, Symb. Antill. **3:** 192. 1902.

*PIPER LINGULAEFOLIUM (p. 3). Hispaniola; Herb. Desv., s.v. C. de Candolle (in Urban, Symb. Antill. **3:** 186. 1902) cited the Hamilton name with a question mark in the synonymy of *Piper angustifolium* Ruiz & Pavon. Moscoso (Catal. Fl. Doming. 128. 1943) accepted *Piper lingulaefolium* Ham.

*PIPER LANCIFOLIUM (p. 3). Jamaica; Herb. Desv., s.v. C. de Candolle (in Urban, Symb. Antill. **3:** 186. 1902) listed the Hamilton name with a question mark in the synonymy of *Piper angustifolium* Ruiz & Pavon from Cuba but not from Jamaica. Adams (Fl. Pl. Jamaica, 1972) does not list the species for Jamaica. The name remains unplaced.

*PIPER SCUTIPHYLLUM (p. 3). Cape Henry, Haiti, v.v. = **Lepianthus peltata** (L.) Raf.; Urban (Symb. Antill. **8:** 152. 1920) cited the Hamilton name with a question mark in the synonymy of *Pothomorphe peltata* L.

*PIPER TILIAEFOLIUM (p. 4). Cayenne; Herb. Desv., s.v. = **Bagassa tiliaefolia** (Desv.) R. Benoist, Arch. Bot. Mém. **1:** 31. 1931. Hamilton suggested this plant might be a new genus. Aublet had published the genus *Bagassa,* and Benoist transferred the species.

*COMMELINA GENICULATA (p. 4). Hispaniola; Herb. Desv., s.v. (P!) = **Commelina geniculata** Ham.; Urban, Symb. Antill. **8:** 94. 1920.

SPOROBOLUS LAMARCKII, "nom. nov." (p. 4). Ind. Occ.; Herb. Desv., s.v. = **Sporobolus poiretii** (Roemer & Schultes) Hitchc.; Hitchcock, Man. ed. 2. 964. 1950.

SPOROBOLUS PURPURASCENS, "comb. nov." (p. 5). Jamaica = **Sporobolus purpurascens** (Sw.) Ham.; Adams, Fl. Pl. Jamaica, 170. 1972.

VILFA VIRGINICA, "comb. nov." (p. 5). Cumana, Jamaica = **Sporobolus virginicus** (L.) Kunth; Hitchcock, Man. ed. 2. 965. 1950.

ERIOCHLOA PUNCTATA, "comb. nov." (p. 5). Jamaica; Herb. Desv., s.v. = **Eriochloa punctata** (L.) Ham.; Adams, Fl. Pl. Jamaica, 180. 1972.

REMIREA MARITIMA (p. 5). Cayenne, Guyana; Herb. Desv., s.v. = **Mariscus pedunculatus** (R. Br.) Koyama; Koyama in Howard, Fl. Lesser Antilles **3:** 279. 1979.

*DIGITARIA SETOSA (p. 6). Antilles; Herb. Desv., s.v. = **Digitaria horizontalis** Willd.; Hitchcock, Man. ed. 2. 854. 1950.

DIGITARIA DISTACHYA, "comb. nov." (p. 6). Antilles; Herb. Desv., s.v. In synonymy Hamilton cited "*Panicum distachyon.* Linn. Mantiss. p. 138?

Lam. Ill. t. 43, f. 2," recognized today as *Panicum distachyon* L., and *Digitaria paspaloides* Michaux, now considered to be a synonym of *Paspalum distichum* L. Without a specimen the Hamilton name can not be placed.

DACTYLOCTENIUM MERIDIONALE, "nom. nov." (p. 6). Carribeis, v.v. = **Dactyloctenium aegyptium** (L.) Beauv. The basionym *Cynosurus aegyptius* L. was cited by Hamilton.

ELEUSINE INDICA, "comb. nov." (p. 6). Jamaica, Nevis, St. Kitts, v.v.; Herb. Desv., s.v. = **Eleusine indica** (L.) Gaertner (1788). The basionym *Cynosurus indicus* L. was cited by Hamilton.

*ORYZA LATIFOLIA (p. 7). Hispanic Hispaniola; Herb. Desv., s.v. = **Oryza latifolia** Desv. Jour. Bot. Desvaux **1:** 77. 1813. In the original description Desvaux stated the locality to be Carolina and Puerto Rico. Hamilton mentioned only Hispaniola.

*OLYRA OVATA (p. 7). Cayenne; Herb. Desv., s.v. = **Ichnanthus panicoides** Beauv.; Chase, Index **2:** 445. 1962.

*PHARUS LANCIFOLIUS (p. 8). Antilles; Herb. Desv., s.v. = **Pharus glaber** HBK.; Hitchcock, Man. Grasses W. I. 152. 1936.

*PHARUS OVALIFOLIUS (p. 8). Antilles; Herb. Desv., s.v. = **Pharus latifolius** L.; Hitchcock, Man. Grasses W. I. 396. 1936.

ANDROPOGON DENSUS, "nom. nov." (p. 8). Antilles; Herb. Desv., s.v. = **Andropogon glomeratus** (Walter) BSP.; Hitchcock, Man. Grasses W. I. 396. 1936.

*ANDROPOGON MICROSTACHYUS (p. 8). Antilles; Herb. Desv., s.v. = **Andropogon condensatus** HBK.; Hitchcock, Man. Grasses W. I. 388. 1936.

*ANDROPOGON VIRGATUS (p. 9). Antilles; Herb. Desv., s.v. = **Andropogon virgatus** Ham.; Hitchcock, Man. Grasses W. I. 393. 1936.

*ANDROPOGON JUNCIFOLIUS (p. 9). Santa Cruz (St. Croix); Herb. Desv., s.v. = **Andropogon gracilis** Sprengel; Hitchcock, Man. Grasses W. I. 389. 1936.

*ECHINOLAENA HIRTA (p. 9). America equinoxiali; Herb. Desv., s.v. = **Echinolaena hirta** Desv. Jour. Bot. Desvaux **1:** 75. 1813. Hamilton cited the locality as Cayenne.

HETEROSTEGA JUNCIFOLIA (p. 9). Jamaica; s.v. = **Bouteloua repens** (HBK.) Scribner & Merr. Gould (in Howard, Fl. Lesser Antilles **3:** 85. 1979) and Hitchcock (Man. Grasses W. I. 139. 1936) follow Urban (Symb. Antill. **4:** 103. 1903) in excluding the synonym of *Aristida americana* L. (*Bouteloua americana* (L.) Scribner) cited by Hamilton. Only *Bouteloua americana* (L.) Scribner is cited by Adams (Fl. Pl. Jamaica, 165. 1972) for Jamaica, while *B. repens* has been attributed to other islands of the Greater Antilles and to St. Martin. No publication has cited herbarium material attributed to Desvaux or Hamilton.

*PANICUM BAMBUSOIDES (p. 10). Puerto Rico; Herb. Desv., s.v. = **Lasiacis**

divaricata (L.) Hitchc.; Hitchcock, Contr. U. S. Natl. Herb. **15:** 16. 1910.

PANICUM LATIFOLIUM, "sp. nov." (p. 10). Antilles; Herb. Desv., s.v. = **Lasiacis sloanei** (Griseb.) Hitchc.; Hitchcock, Bot. Gaz. **51:** 302. 1911.

*PANICUM SORGHOIDEUM (p. 10). Puerto Rico; Herb. Desv., s.v. = **Lasiacis sorghoidea** (Desv.) Hitchc. & Chase, Contr. U. S. Natl. Herb. **18:** 338. 1917.

*PANICUM AGROSTIDIFORME (p. 10). Puerto Rico; Herb. Desv., s.v. = **Panicum laxum** Sw.; Urban, Symb. Antill. **4:** 91. 1903.

*PANICUM ORNATUM (p. 11). Puerto Rico; Herb. Desv., s.v. = **Panicum acuminatum** Sw.; Hitchcock, Man. Grasses W. I. 285. 1936.

*PANICUM PORTORICENSE (p. 11). Puerto Rico; Herb. Desv., s.v. = **Panicum portoricense** Ham.; Hitchcock, Man. Grasses W. I. 289. 1936.

PANICUM CAYENNENSE, "sp. nov." (p. 11). Cayenne; Herb. Desv., s.v. = **Panicum cayennense** Lam.; Hitchcock, Man. Grasses W. I. 257. 1936.

*PENNISETUM ALOPECUROIDES (p. 11). Ind. Occ.; Herb. Desv., s.v. = **Pennisetum setosum** (Sw.) L. C. Rich. ex Pers.; Hitchcock, Man. Grasses W. I. 357. 1936.

*PENNISETUM ERUBESCENS (p. 11). St. Thomas; Herb. Desv., s.v. = **Pennisetum setosum** (Sw.) L. C. Rich. in Pers.; Hitchcock, Man. Grasses W. I. 357. 1936.

*RHYTACHNE ROTTBOELLIOIDES (p. 12). Antilles; Herb. Desv., s.v. = **Rhytachne rottboellioides** Ham.; Hitchcock (Man. Grasses W. I. 417. 1936) suggested, "The locality given is probably an error as with many other Desvaux specimens. The specimen could not be found in the Paris Herbarium." The taxon has not been reported elsewhere in the West Indian flora but is included in tropical African floras.

*SORGHUM PARVIFLORUM (p. 12). Hispaniola; Herb. Desv., s.v. = **Sorghastrum setosum** (Griseb.) Hitchc.; Hitchcock, Contr. U. S. Natl. Herb. **12:** 195. 1909. According to Moscoso (Catal. Fl. Doming. 40. 1943), this is not *Sorghum parviflorum* Beauv. (1812).

*CYPERUS UNCINATUS (p. 12). Cayenne, Insulis Carribeis; Herb. Desv., s.v. = **Cyperus uncinatus** Poiret in Lam.; Urban, Symb. Antill. **2:** 24. 1900.

*CYPERUS FASTUOSUS (p. 12). Puerto Rico; Herb. Desv., s.v. = **Torulinium odoratum** (L.) Hooper; Hooper, Kew Bull. **26:** 579. 1972.

*CYPERUS POEOIDES (p. 12). Haiti, v.v.; Herb. Desv., s.v. = **Torulinium odoratum** (L.) Hooper. Urban (Symb. Antill. **2:** 54. 1900) referred this name to the synonymy of *T. confertum*, which Hooper (Kew Bull. **26:** 579. 1972) considers a synonym of *T. odoratum* (L.) Hooper.

CYPERUS HYDRA, "sp. nov." (p. 13). Carribeis, v.v. = **Cyperus rotundus** L.; Urban, Symb. Antill. **2:** 35. 1900.

KYLLINGIA VAGINATA (p. 13). Jamaica, Hispaniola; Herb. Desv., s.v. = **Kyllingia peruviana** Lam.; Urban, Symb. Antill. **8:** 53. 1920.

NEMUM SPADICEUM, "comb. nov." (p. 13). Hispaniola; Herb. Desv., s.v. = **Scirpus angolensis** C. B. Clarke var. **brizaeformis** (Hutch.) Hooper, Kew Bull. **26:** 580. 1972.

*FIMBRISTYLIS DIVARICATUS (p. 14). Puerto Rico; Herb. Desv., s.v. = **Fimbristylis divaricatus** Ham. Urban (Symb. Antill. **2:** 84. 1900, and *ibid.* **4:** 119. 1903) listed this name among "species residuae" and "species dubiae," respectively. Britton and Wilson (Sci. Survey Porto Rico Virgin Is. **5:** 96. 1920) noted, "The specimen in the herbarium of Desvaux not identified by modern botanists, the description being incomplete."

*FIMBRISTYLIS HIRTELLUS (p. 14). Puerto Rico; Herb. Desv. s.v. = **Fimbristylis hirtellus** Ham. Urban (Symb. Antill. **2:** 84. 1900) listed this among "species residuae." As with the previous species, Britton and Wilson (Sci. Survey Porto Rico Virgin Is. **5:** 96. 1920) could not place this one. A. Gonzales Mas (Cyperaceae of Puerto Rico, Unpubl. Ph.D. Thesis, Louisiana State Univ. p. 200. 1964) listed *F. divaricatus* and *F. hirtellus* as "excluded species."

*FIMBRISTYLIS SPARTIUM (p. 14). Antilles; Herb. Desv., s.v. = **Fimbristylis spartium** Ham. Urban (Symb. Antill. **2:** 84. 1900) listed this name among "species residuae." Neither Britton and Wilson (Sci. Survey Porto Rico Virgin Is. Vol. 5. 1920) nor Gonzales Mas (Cyperaceae Puerto Rico. 1964) considered the name.

SCIRPUS DOMINGENSIS (p. 14). Hispaniola; Herb. Desv., s.v. = **Fimbristylis spadicea** Vahl. Urban (Symb. Antill. **2:** 79. 1900) noted that the name Hamilton used had been published by Persoon in 1805. The Persoon reference was cited in the bibliography Hamilton published.

*SCIRPUS STANS (p. 14). Ind. Occ.; Herb. Desv., s.v. = **Fimbristylis ferruginea** Vahl; Urban, Symb. Antill. **2:** 78. 1900.

*ZOSTEROSPERMUM GRACILE (p. 14). Ind. Occ.; Herb. Desv., s.v. = **Rhynchospora micrantha** Vahl; Kükenthal, Bot. Jahrb. **75:** 274. 1951.

*RHYNCHOSPORA GLOBOSA (p. 15). Cayenne; Herb. Desv., s.v. = **Rhynchospora barbata** (Vahl) Kunth ex Kükenthal; Kükenthal, Bot. Jahrb. **74:** 485. 1949.

*RHYNCHOSPORA CONICA (p. 15). Cayenne; Herb. Desv., s.v. = **Rhynchospora cephalotes** (L.) Vahl; Kükenthal, Bot. Jahrb. **75:** 122. 1950.

*RHYNCHOSPORA PYRAMIDATA (p. 15). Jamaica; Herb. Desv., s.v. = **Rhynchospora polyphylla** Vahl; Kükenthal, Bot. Jahrb. **74:** 403. 1949.

*TORULINIUM CONFERTUM (p. 15). Cayenne; Herb. Desv., s.v. = **Torulinium odoratum** (L.) Hooper; Hooper, Kew Bull. **26:** 579. 1972.

DICHROMA CILIATUM, "nom. nov." (p. 15). Dodand (St. Kitts), Nevis, v.v. and s.v. = **Rhynchospora stellata** (Lam.) Griseb.; T. Koyama in Howard, Fl. Lesser Antilles **3:** 287. 1979.

*ERIOCAULON PLANTAGINIOIDES (p. 16). Guyana; Herb. Desv., s.v. = **Paepalanthus plantaginioides** (Ham.) Koern. in Martius, Fl. Brasil. **3**(1)**:** 470. 1863; Moldenke, Fifth Summary **2:** 956. 1971.

*POTHOS SCOLOPENDRINUS (p. 16). Guyana; Herb. Desv., s.v. = **Anthurium gracile** (Rudge) Lindley. Simon Mayo, of the Royal Botanic Garden, Kew, has indicated that this synonymy will be adopted for the treatment of the Araceae in the *Flora of Trinidad and Tobago*.

PERAMA HIRSUTA (p. 16). Guyana; Herb. Desv., s.v. = **Perama hirsuta** Aublet. Aublet was cited in synonymy by Hamilton.

CATESBAEA SPINOSA (p. 17). Bahamas; Herb. Desv., s.v. = **Catesbaea spinosa** L. Sp. Pl. **1:** 109. 1753.

COCCOSYPSILUM BROWNEI, "nom. nov." (p. 17). Jamaica; Herb. Desv., s.v. = **Coccocypselum herbaceum** Aublet; Moore & Rendle in Fawcett & Rendle, Fl. Jamaica **8:** 42. 1936. This name does not appear in *Index Kewensis* or in *Index Nominum Genericorum* as an orthographic variant.

*COCCOSYPSILUM CHRYSOPHYLLOIDES (p. 17). Ind. Occ.; Herb. Desv., s.v. This name is not in *Index Kewensis* and has not been found in any publication I have consulted.

COCCOSYPSILUM CONDALEA, "nom. nov." (p. 17). Caracas; Herb. Desv., s.v. = **Coccocypselum lanceolatum** (Ruiz & Pavon) Pers.; Steyermark, Fl. Venezuela **9:** 488. 1974.

COCCOSYPSILUM TONTANEA, "nom. nov." (p. 18). Caracas; Herb. Desv., s.v. This name can not be placed. Hamilton cited in synonymy *Bellardia repens* Willd. (= *C. tontanea* HBK.; Steyermark, Fl. Venezuela **9:** 484. 1974) and *Tontanea guianensis* Aublet (= *C. guianense* (Aublet) K. Schum.; Steyermark, Fl. Venezuela **9:** 481. 1974).

PAVETTA COFFEOIDES, "comb. nov." (p. 18). St. Kitts, Nevis, v.v.; Herb. Desv., s.v. = **Faramea occidentalis** (Jacq.) A. Rich.; Fawcett & Rendle, Fl. Jamaica **8:** 80. 1936. The Hamilton binomial does not appear in *Index Kewensis*.

SCOLOSANTHUS VERSICOLOR (p. 18). Santa Cruz (St. Croix); Herb. Desv., s.v. = **Scolosanthus versicolor** Vahl. The Vahl binomial was cited by Hamilton.

COUTOUBAEA PURPUREA, "nom. nov." (p. 18). Guyana; Herb. Desv., s.v. = **Coutoubaea ramosa** Aublet. The Aublet name was cited by Hamilton.

COUTOUBAEA SPICATA, "comb. nov." (p. 19). Guyana; Herb. Desv., s.v. = **Coutoubaea spicata** Aublet; Lemée, Fl. Guyane Fr. **3:** 279. 1953.

BOUVARDIA AMERICANA, "nom. nov." (p. 19). Jamaica; Herb. Desv., s.v. = **Bouvardia ternifolia** (Cav.) Schlecht.; Standley, Contr. U. S. Natl. Herb. **23:** 1362. 1926.

EVEA GUIANENSIS (p. 19). Guyana = **Faramea guianensis** (Aublet) Bremek.; Bremekamp, Rec. Trav. Bot. Néerl. **31:** 279. 1934.

*EXACUM VERTICILLATUM (p. 19). Hispaniola; Herb. Desv., s.v. = **Enicostema verticillatum** (L.) Engler ex Gilg in Engler & Prantl, Nat. Pflanzenfam. IV. **2:** 67. 1895.

*LYGISTUM AXILLARE (p. 20). Hispaniola; Herb. Desv., s.v. = **Manettia lygistum** (L.) Sw. Gillis could not find this specimen.

LYGISTUM SPICATUM (p. 20). Martinique, Cumana, Santa Cruz (St. Croix), Haiti, v.v.; Herb. Desv., s.v. = **Gonzalagunia** spp. Hamilton cited *Coccosypsilum spicatum* Humb. (Nov. Gen. **3:** 406 [error for 317]. 1820) and *Barleria hirsuta* Jacq. (Select. Stirp. Am. Hist. 231. 1763; Pl. Am. Pict. *t. 172.* 1763). The genus is in need of a revision, and there is a question whether the Humboldt material from Cumana and the Jacquin species from Martinique are the same species. No specimens have been located.

MYRMECIA SCANDENS (p. 21). Guyana = **Tachia guianensis** Aublet. Hamilton cited the Aublet name.

*FAGARA MICROPHYLLA (p. 21). St. Kitts, v.v.; Herb. Desv., s.v. = **Zanthoxylum spinifex** (Jacq.) DC.; Britton & Wilson, Sci. Survey Porto Rico Virgin Is. **5:** 450. 1924.

FAGARA PTEROTA (p. 22). Hispaniola, St. Kitts, Nevis, v.v. and s.v. = **Zanthoxylum fagara** (L.) Sarg. The type of the basionym *Schinus fagara* L. is Sloane, Voyage **2:** *pl. 162, fig. 1,* cited in synonymy by Hamilton.

FAGARA TRAGODES (p. 22). Nevis, Haiti, Hispaniola = **Zanthoxylum tragodes** (L.) DC. Moscoso (Catal. Fl. Doming. 283. 1943) regarded this species as endemic to Hispaniola.

*ALTERNANTHERA FILAGINOIDES (p. 23). Hispaniola; Herb. Desv., s.v. (P) = **Guilleminea lanuginosa** (Poiret) Hooker. Urban (Symb. Antill. **8:** 204. 1920) referred the Hamilton name to *Guilleminea* with a question mark. The specimen in Paris has been annotated recently by James Mears.

CORDIOPSIS MIRABILLOIDES (p. 23). Hispaniola; Herb. Desv., s.v. = **Cordia serrata** (L.) Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. **3:** 83. 1893. The binomial Hamilton used was published by Desvaux (Jour. Bot. Desvaux **1:** 167. 1808).

CORDIA TOQUEVA (p. 23). Guyana; Herb. Desv., s.v. = **Cordia toqueve** Aublet. Hamilton noted that the specimen in Herb. Desvaux was slightly different and might be a variety. The material has not been seen or cited by recent botanists as far as can be determined.

*CORDIA NITIDA (p. 23). Hispaniola; Herb. Desv., s.v. = **Cordia nitida** Vahl; Urban, Symb. Antill. **8:** 577. 1921. Gillis could not find this material.

*TOURNEFORTIA LUCIDA (p. 24). Antilles; Herb. Desv., s.v. = **Tournefortia lucida** Ham. This name has not been considered by recent monographers. The name is without an assignment in the original *Index Kewensis.*

*TOURNEFORTIA MICROPHYLLA (p. 24). Antilles; Herb. Desv., s.v. = **Tournefortia volubilis** L.; Urban, Symb. Antill. **8:** 587. 1921. *Tournefortia microphylla* Bert. (in Sprengel, Syst. Veg. **1:** 644. 1825) probably antedates the Hamilton name by several months.

*CONVOLVULUS ALATUS (p. 24). Tobago = **Operculina alata** (Ham.) Urban, Symb. Antill. **3:** 343. 1902.

*CONVOLVULUS NEVISIENSIS (p. 24). Nevis, v.v. Hamilton compared this species, which has small, blue flowers, with *C. verticillata* and *C. nodiflora,*

names now placed in the genus *Jacquemontia*. K. Robertson, who has monographed this genus, had not located material and could not place the plant from the description that was compiled from living material. It is possible that no herbarium specimen was prepared, although in the original *Index Kewensis* the name is referred to *Jacquemontia hirsuta*.

*IPOMOEA LEUCANTHA (p. 25). Cuba?, Ind. Occ.; Herb. Desv., s.v. = **Ipomoea leucantha** Jacq. Collect. **2:** 280. 1789, which antedates Hamilton's new species. Hamilton cited Cuba with a question mark; León and Alain (Fl. Cuba **4:** 244. 1957) stated that this is a South American species and the reference to Cuba was probably an error. A solitary specimen in the Gray Herbarium was prepared in 1870 from material grown from seed obtained from "hort. Paris." Filed under "South America," it has not been annotated by recent scholars.

*CAPSICUM VIOLACEUM (p. 25). Nevis, v.v. Hamilton obtained living material from Nevis and cited the listing in Catal. Horti Paris. 70, *sine descr.* The name has not been placed by modern workers.

*CESTRUM ALATERNOIDES (p. 25). Antilles; Herb. Desv., s.v. = **Cestrum laurifolium** L'Hér. Hamilton cited Catal. Horti Paris, 70, *sine descr.* Schulz (in Urban, Symb. Antill. **6:** 257. 1909) credited the Hamilton binomial to Desfontaines. Gillis could not find a specimen, and none was cited by Francey (Candollea **6:** 335–9. 1935).

SOLANUM DESVAUXII, "nom. nov." (p. 26). Antilles (Nevis?), v.v.; Herb. Desv., s.v. = **Solanum americanum** Miller. Hamilton cited "*S. nodiflorum* Herb. Desv." Schulz (in Urban, Symb. Antill. **6:** 162. 1909) placed the Hamilton name in the synonymy of *Solanum nigrum* var. *americana* (Miller) Schulz. The modern nomenclature for this complex is not satisfactory for floristic work.

*ARDISIA OBOVATA (p. 26). Hispaniola; Herb. Desv., s.v. (P!) = **Ardisia obovata** Ham. Urban (Symb. Antill. **2:** 397. 1901) accepted the Hamilton binomial but noted "nec Blume." Blume's homonym, published on p. 688 of *Bijdragen tot de Flora van Nederlandsch Indië,* was issued in 1826 (Reg. Veg. **52:** 37. 1967) although the date on the title page is 1825.

*PLUMERIA TUBERCULATA (p. 26). Haiti = **Plumeria tuberculata** Lodd. This name was accepted by Moscoso (Catal. Fl. Doming. 498. 1943), although Woodson (N. Am. Fl. **19**(2)**:** 117. 1938) listed it in the synonymy of *Plumeria obtusa* L. var. *sericifolia* (C. Wright) Woodson. In the preface to the *Prodromus* (p. vii), Hamilton took credit for introducing the plant to cultivation.

THEOPHRASTA HENRICI, "nom. nov." (p. 27). Haiti = **Theophrasta jussiaei** Lindley; Urban, Symb. Antill. **8:** 517. 1920. Hamilton obtained living material of this plant and introduced it to cultivation in Europe.

*CYPELLIUM NERVOSUM (p. 28). Guyana; Herb. Desv., s.v. = **Styrax** sp. Airy Shaw (in Willis, Dict. Fl. Pl. ed. 8. 330. 1973) equates to *Styrax* L. the generic name attributed to Desvaux. The binomial was not considered

by Perkins in her monograph (in Engler, Pflanzenr. IV. **241:** 1–111. 1907). No material has been located or cited as far as I can determine.

*ETERICIUS PARASITICUS (p. 28). Guyana; Herb. Desv., s.v. Rubiaceae? Airy Shaw (in Willis, Dict. Fl. Pl. ed. 8. 436. 1973) attributes the generic name to Desvaux and states "Rubiaceae (inc. sed.)." Hamilton said the leaves were alternate. The plant has not been cited in modern publications, and no specimens are known.

ARACHNIMORPHA INCANA, "comb. nov." (p. 28). Jamaica; Herb. Desv., s.v. = **Rondeletia incana** Sw. Moore (in Fawcett & Rendle, Fl. Jamaica **8:** 29. 1936) cited the Hamilton binomial in synonymy with a question mark. The Hamilton name is not in *Index Kewensis*.

*PALICURIA CAJANNENSIS (p. 29). Cayenne; Herb. Desv., s.v. = **Palicourea pedunculosa** DC.; Lemée, Fl. Guyane Fr. **3:** 545. 1953.

*PALICURIA CROCEOIDES (p. 29). Antilles; Herb. Desv., s.v. In the original *Index Kewensis* this name was equated with *Palicourea crocea* (Sw.) Roemer & Schultes with a question mark. The name remains unplaced by recent workers.

*EMMOTUM FAGIFOLIUM (p. 29). Guyana; Herb. Desv., s.v. (P!) = **Emmotum fagifolium** Ham.; Lemée, Fl. Guyane Fr. **2:** 315. 1952.

*ECHITES OBLONGIFOLIA (p. 30). Guyana; Herb. Desv., s.v. Woodson (Ann. Missouri Bot. Gard. **23:** 243. 1936) stated that this plant is "perhaps referable to *Mesechites*." The name has not been placed otherwise.

ECHITES QUINQUANGULARIS (p. 30). Tobago, v.v. = **Prestonia quinquangularis** (Jacq.) Sprengel; Woodson, N. Am. Fl. **29**(2)**:** 181. 1938.

*ECHITES BARBATA (p. 30). Ind. Occ.; Herb. Desv., s.v. = **Urechites lutea** (L.) Britton; Urban, Symb. Antill. **8:** 547. 1920; Woodson, N. Am. Fl. **29**(2)**:** 170. 1938.

*ECHITES CHRISTOPHORIANA (p. 31). St. Kitts, v.v. Woodson (N. Am. Fl. **29**(2)**:** 176. 1938) suggested that this may be *Mesechites repens* (Jacq.) Miers; however, that species is considered to be endemic to Hispaniola. A coastal plant with yellow flowers from Basse Terre, St. Kitts, would probably be *Urechites lutea* (L.) Britton.

*ECHITES CONCOLOR (p. 31). Hispaniola; Herb. Desv., s.v. Urban (Symb. Antill. **8:** 546. 1920) assigned this name to the synonymy of *Rhabdadenia paludosa* (Vahl) Miers with a question mark. Woodson (Ann. Missouri Bot. Gard. **23:** 232. 1936) stated that this "may refer to *Mesechites angustifolia* (Poiret) Miers."

*ECHITES LINEARIFOLIA (p. 31). Haiti, v.v.; Herb. Desv., s.v. = **Mesechites angustifolia** (Poiret) Miers; Woodson, Ann. Missouri Bot. Gard. **23:** 239. 1936. Urban (Symb. Antill. **8:** 545. 1921) stated that he had seen a photograph of the original specimen.

*GONOLOBUS STAPELIOIDES (p. 32). Tobago, v.v.; Herb. Desv., s.v. = **Gonolobus stapelioides** Ham. Schlechter (in Urban, Symb. Antill. **1:** 283. 1899) commented that this is a Jamaican species and that the location Hamilton

cited as Alfred Hall near Scarborough, Tobago, must be an error. His comments suggest that he must have seen a specimen. Adams (Fl. Pl. Jamaica, 597. 1972) also considers this species endemic to Jamaica.

*GONOLOBUS VIRESCENS (p. 32). Jamaica; Herb. Desv., s.v. (P!). Schlechter (in Urban, Symb. Antill. **1:** 290. 1899) listed this name in a category of "Species non satis notae v. mihi non visae." However, he noted that the flower on the plant he studied had been destroyed, so a more accurate description could not be compiled. He suggested that the labels had been switched: *G. virescens* was from Tobago, while *G. stapelioides* was from Jamaica.

The Hamilton binomial was not listed in *Index Kewensis*. *Gonolobus virescens* Decaisne (in DC. Prodr. **8:** 596. 1844), based on *Galeotti 1552* (from Mexico), is a later homonym and probably requires a new name.

*RHUS RUFESCENS (p. 32). Jamaica; Herb. Desv., s.v. (P!) = **Brunella comocladifolia** Humb. & Bonpl.; Urban (Symb. Antill. **6:** 102. 1909) indicated the correct identification for this plant, and Gillis found the specimen that had been annotated by Urban in 1908.

*TURNERA HIRTA (p. 33). Guyana; Herb. Desv., s.v. Urban (Jahrb. Bot. Gart. Berlin **2:** 147. 1853) did not see this material while preparing his monograph. He noted that the name was a later homonym of *T. hirta* Willd. De Candolle (Prodr. **3:** 348. 1828) renamed the Desvaux material **Turnera desvauxii** DC.

*TURNERA MICROPHYLLA (p. 33). Hispaniola; Herb. Desv., s.v. = **Turnera diffusa** Willd. ex Schultes; Urban, Symb. Antill. **8:** 449. 1920. Gillis suggested that *Triacis microphylla* Griseb. (Fl. Brit. W. Indian Is. 297. 1860), a new combination based by implication on "*Turnera* Desv.," needs to be reexamined and may be a distinct species typified by a Swainson collection from the Bahamas.

*LORANTHUS ANCEPS (p. 33). Guyana; Herb. Desv., s.v. (P!) = **Oryctanthus florulentus** (Rich.) Urban. Urban (Bot. Jahrb. **24:** 31. 1897) reported that Van Tiegham had seen the specimen and had confirmed the determination.

*LORANTHUS DOMINGENSIS (p. 33). Hispaniola; Herb. Desv., s.v. = **Phoradendron trinervium** (Lam.) Griseb. var. **domingense** (Ham.) Krug & Urban. Urban (Bot. Jahrb. **24:** 38. 1897) implied that he had seen a specimen in Paris.

*LORANTHUS LAXIFLORUS (p. 33). Hispaniola; Herb. Desv., s.v. = **Dendropemon laxiflorus** (Desv.) Steudel. Moscoso (Catal. Fl. Doming. 156. 1943) used this name, while Urban (Symb. Antill. **8:** 184. 1920) used *Phthirusa laxiflora* (Desv.) Eichler.

*BALANTIUM CORDIFOLIUM (p. 34). Guyana; Herb. Desv., s.v. (P!) = **Parinari campestris** Aublet. Prance (Fl. Neotrop. Monogr. **9:** 181. 1972) accepted this determination and cited a flowering specimen in Paris.

*AMYRIS? HEXANDRA (p. 34). Nevis, v.v. = **Dacryodes excelsa** Vahl; Rose, N. Am. Fl. **25**(3): 258. 1911. Hamilton referred to this plant flowering on Nevis in June and September (an entry was probably drawn from field notes).

*COMBRETUM PYRAMIDATUM (p. 35). Guyana; Herb. Desv., s.v. (P!) = **Combretum pyramidatum** Ham. Exell (Jour. Linn. Soc. Bot. **55:** 126. 1953) accepted this species and saw a type in Paris.

*RHEXIA AUREA (p. 35). Antilles; Herb. Desv., s.v. = **Rhexia lutea** Michaux; Cogniaux in DC. Monogr. Phanerog. **7:** 388. 1891. More recently, James (Brittonia **8:** 216. 1956) did not cite this name and considered *R. lutea* to be restricted to the United States.

*RHEXIA LINEARIFOLIA (p. 35). Antilles; Herb. Desv., s.v. = **Rhexia mariana** L. Cogniaux (in DC. Monogr. Phanerog. **7:** 388. 1891) made this placement with a question. The Hamilton name was not listed by James in his revision of the genus (Brittonia **8:** 216. 1956). A specimen has been seen by Philcox, who determined it to be *Angelonia angustifolia* Bentham.

RHEXIA AQUATICA, "comb. nov." (p. 35). Cayenne, Dominica, Jamaica, Guadeloupe, v.v. and s.v. = **Nepsera aquatica** (Aublet) Naudin; Urban, Symb. Antill. **8:** 490. 1920.

RHEXIA INCONSTANS, "nom. nov." (p. 36). St. Kitts, Guadeloupe, v.v. and s.v. = **Tibouchina ornata** (Sw.) Baillon; Howard, Jour. Arnold Arb. **53:** 399. 1972.

*RHEXIA TETRAPTERA (p. 36). Cayenne; Herb. Desv., s.v. = **Rhexia stricta** Pursh, according to Cogniaux in DC. Monogr. Phanerog. **7:** 387. 1891. James (Brittonia **8:** 227. 1956) listed *Rhexia stricta* Pursh in the synonymy of *R. virginica* var. *purshii* (Sprengel) James but noted that it is "not *R. stricta* Bonpl. Melast. II. Rhex. 19, *pl. 8.* 1807." This name has not been placed satisfactorily.

THYANA SIMPLICIFOLIA, "comb. nov." (p. 36). Hispaniola = **Thouinia simplicifolia** Poit.; Urban, Symb. Antill. **8:** 391. 1920. The Hamilton binomial was not listed in *Index Kewensis*.

THYANA TRIFOLIATA, "comb. nov." (p. 36). Hispaniola, Jamaica = **Thouinia trifoliata** Poit.; Urban, Symb. Antill. **8:** 391. 1920. The Hamilton binomial was not listed in *Index Kewensis*.

*SAPINDUS LUCIDUS (p. 36). Hispaniola; Herb. Desv., s.v. = **Exothea paniculata** (Juss.) Radlk.; Urban, Symb. Antill. **8:** 396. 1920.

*LAURUS GEMINIFLORA (p. 37). St. Kitts, Jamaica, v.v.; Herb. Desv., s.v. This name has not been placed in the Lauraceae. Kostermans listed it in his *Bibliographia Lauracearum* (1964, p. 627), although previously (Rec. Trav. Bot. Néerl. **33:** 757. 1936) he had stated, "*Laurus geminiflora* Desv. in Hamilt. Prodr. Fl. Ind. Occ. (1825) p. 37 does, according to the description, not correspond either with *Phyllostemonodaphne* or with *Systemonodaphne*." In a later reference (*ibid.* **35:** 105. 1938) he created *Systemonodaphne mezii* Kosterm., with the synonym "*Systemonodaphne geminiflora* Mez in Jahrb. Bot. Garten Berlin V: 79. 1889 (excl. cit. syn. *Laurus geminiflora* Desv.)."

*SAMYDA PUBESCENS (p. 37). Hispaniola; Herb. Desv., s.v. = **Casearia aculeata** Jacq.; Urban, Symb. Antill. **8:** 446. 1920.

*MELASTOMA CHRISTOPHORIANA (p. 37). St. Kitts, v.v. = **Tetrazygia discolor** (L.) DC.; Cogniaux in DC. Monogr. Phanerog. **7:** 721. 1891.

*MELASTOMA DODANDIANA (p. 37). Dodand (St. Kitts), Nevis, v.v. = **Charianthus nodosus** (Desr.) Triana; Cogniaux in DC. Monogr. Phanerog. **7:** 716. 1891.

*CASSIA DISCOLOR (p. 38). Jamaica; Herb. Desv., s.v. = **Cassia glauca** Lam.; Bentham, Trans. Linn. Soc. London **27:** 555. 1871. The Hamilton name had been published previously by Desvaux (Jour. Bot. Desvaux **3:** 73. 1814).

*CASSIA HIRSUTA (p. 38). Jamaica; Herb. Desv., s.v. = **Cassia cathartica** Martius; Bentham in Martius, Fl. Brasil. **15**(2)**:** 155. 1870. Adams (Fl. Pl. Jamaica, 1972) does not list *C. cathartica* from Jamaica.

CATHARTOCARPUS BICAPSULARIS, "comb. nov." (p. 38). St. Kitts, Nevis, v.v. = **Cassia bicapsularis** L. Hamilton cited the Linnaean name. The Hamilton binomial was not cited in *Index Kewensis*.

GONOCARPUS JACQUINI, "nom. nov." (p. 39). Carthagena = **Combretum decandrum** Jacq.; Exell, Jour. Linn. Soc. Bot. **55:** 133. 1953.

BANISTERIA LAURIFOLIA (p. 39). Nevis, v.v. = **Heteropteris laurifolia** (L.) Juss.; Niedenzu in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 457. 1928.

*BANISTERIA MAGNOLIAEFOLIA (p. 40). Guyana; Herb. Desv., s.v. = **Heteropteris platyptera** DC. Niedenzu (in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 457. 1928) referred the Hamilton name to *Heteropterys longifolia* (Sw.) Niedz. (1903), which is a later homonym of *H. longifolia* HBK. (1822).

BANISTERIA MICROPHYLLA, "sp. nov." (p. 40). Nevis, v.v. = **Stigmaphyllon lingulatum** (Poiret) Small, N. Am. Fl. **25**(2)**:** 140. 1910. Niedenzu (in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 457. 1928) referred the Hamilton name to *Stigmaphyllon periplocifolia* (Desf.) Juss. The Desfontaines basionym is a *nomen nudum* and was not published validly until 1825. Small's nomenclature is correct.

*BANISTERIA CALCITRAPA (p. 40). Guyana; Herb. Desv., s.v. = **Stigmaphyllon ovatum** (Cav.) Niedz. in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 455. 1928.

*BANISTERIA DEFORMIS (p. 40). Antilles; Herb. Desv., s.v. = **Stigmaphyllon angulosum** (L.) Juss.; Niedenzu in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 493. 1928.

BANISTERIA TOMENTOSA, "sp. nov." (p. 40). Insulis Carribeis; Herb. Desv., s.v. = **Stigmaphyllon tomentosum** (Desf.) Niedz. in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 459. 1928. The Niedenzu name should be corrected to *Stigmaphyllon tomentosum* (Ham.) Niedz.

*MALPIGHIA ELLIPTICA (p. 40). Ind. Occ.; Herb. Desv., s.v. = **Heteropteris purpurea** (L.) Kunth; Niedenzu in Engler, Pflanzenr. IV. **141**(Heft 93)**:** 322. 1928.

MALPIGHIA BIFLORA (p. 41). Antilles; Herb. Desv., s.v. = **Malpighia biflora** Poiret in Lam.; Urban, Symb. Antill. **8:** 338. 1920.

MALPIGHIA PUNICIFOLIA (p. 41). Hispaniola; Herb. Desv., s.v. = **Malpighia emarginata** Sessé & Moç. ex DC. José L. Vivaldi's work on this complex of species awaits publication.

MALPIGHIA MACROPHYLLA (p. 41). Ind. Occ. = **Malpighia fucata** Ker-Gawl.; Britton & Wilson, Sci. Survey Porto Rico Virgin Is. **5:** 443. 1924.

*MALPIGHIA TINIFOLIA (p. 41). Hispaniola; Herb. Desv., s.v. = **Prionostemma aspera** (Lam.) Miers. Niedenzu (in Engler, Pflanzenr. IV. **141**(Heft 94)**:** 642. 1928) stated that the Hamilton plant was *Hippocratea aspera* Lam. (= *Prionostemma aspera* (Lam.) Miers). Smith, in his monograph of the Hippocrateaceae (Brittonia **3:** 393. 1940) did not cite the Hamilton name. He recognized a single species for this genus, which does not occur in Hispaniola but ranges from Panama to Trinidad and into Brazil.

*XYLADENIUS GLANDULOSUS (p. 41). Guyana; Herb. Desv., s.v. = **Banara guianensis** Aublet; Tulasne (Ann. Sci. Nat. III. **7:** 290. 1847) suggested this identification. Sleumer has annotated all specimens labeled *Banara glandulosa* as *B. guianensis* Aublet.

*TRIUMFETTA ULMIFOLIA (p. 41). Ind. Occ.; Herb. Desv., s.v. = **Triumfetta semitriloba** Jacq. This reference is made in *Index Kewensis*. The Hamilton name was not considered by K. K. Lay in his monograph of the genus (Ann. Missouri Bot. Gard. **37:** 315–395. 1950).

APATITIA BLAKEOIDES, "nom. nov." (p. 42). Guyana; Herb. Desv., s.v. = **Bellucida grossularioides** (L.) Triana. *Bellucida* Raf. is conserved over *Apatitia* Desv. ex Ham. (Reg. Veg. **97:** 375. 1938); *Blakea quinquenervia* Aublet, cited in synonymy by Hamilton, is listed as a synonym of *Bellucida grossularioides*.

PEDILANTHUS PADIFOLIUS (p. 42). Barbados, Nevis, v.v. = **Pedilanthus tithymaloides** (L.) Poit. subsp. **padifolius** (L.) Dressler, Contr. Gray Herb. **182:** 156. 1951.

PEDILANTHUS TITHYMALOIDES (p. 43). Haiti, v.v. = **Pedilanthus tithymaloides** (L.) Poit.; Dressler, Contr. Gray Herb. **182:** 1951.

*EUGENIA RAMIFLORA (p. 43). Guyana; Herb. Desv., s.v. = **Eugenia ramiflora** Ham. De Candolle (Prodr. **3:** 285. 1828) could not place this species, but the name was accepted by Lemée (Fl. Guyane Fr. **3:** 159. 1953).

EUGENIA TRIFLORA, "comb. nov." (p. 44). Carthagena. Hamilton cited *Myrtus triflora* Jacq. in synonymy. De Candolle (Prodr. **3:** 274. 1828) listed Jacquin's name under *Eugenia* with a question mark as "*M. triflora* Jacq. Stirp. 153, t. 193, f. 59, not Spreng." The Hamilton binomial was not listed in *Index Kewensis* and antedates the same name by Sessé & Moçino (Pl. Novae Hisp. ed. 1. 83. 1887–1890).

*EUGENIA PYRIFOLIA (p. 44). Guyana; Herb. Desv., s.v. De Candolle (Prodr. **3:** 285. 1828) accepted this species in *Eugenia*. Lemée (Fl. Guyane Fr. **3:** 145. 1953) cited *Myrcia pyrifolia*?, implying a new combination.

MYRTUS PSIDIOIDES (p. 44). Ind. Occ.; Herb. Desv., s.v. De Candolle (Prodr. **3:** 242. 1828) cited "*M*[*yrtus*]? *psidioides* Desv. in Hamilton," with the

opinion that it might be a species of *Myrcia*. Berg (Linnaea **27:** 198. 1856) supplied the new name *Eugenia desvauxiana* Berg, citing Hamilton in synonymy. Lemée (Fl. Guyane Fr. **3:** 162. 1953) accepted "*Eugenia psidioides* DC."

*MYRTUS UMBELLATA (p. 45). Guyana; Herb. Desv., s.v. De Candolle (Prodr. **3:** 242. 1828) listed "*M*[*yrtus*]? *umbellata* Desv.," with the statement that it might be a *Myrcia*.

MYRTUS CUMETE, "comb. nov." (p. 45). Guyana = **Myrcia coumete** (Aublet) DC.; Lemée, Fl. Guyane Fr. **3:** 145. 1953.

MYRTUS DIVARICATA, "comb. nov." (p. 45). Martinique. This name is not placed. Urban (Bot. Jahrb. **19:** 585. 1895) assigned the Hamilton name to the synonymy of *Myrcia berberis* DC. with a question mark and excluded Hamilton's synonym, *Eugenia divaricata* Lam. Encycl. **3:** 202. 1789. An entry in *Index Kewensis* noted that *Eugenia divaricata* Berg (1854) is a later homonym of *Eugenia divaricata* Bentham (1840).

MYRTUS GUIANENSIS, "comb. nov." (p. 45). Guyana = **Myrcia guianensis** (Aublet) DC.; Lemée, Fl. Guyane Fr. **3:** 148. 1953.

*PARALIA GUIANENSIS (p. 45). Guyana; Herb. Desv., s.v. = **Diospyros guianensis** (Aublet) Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. **1:** 163. 1891. Accepted by Lemée, Fl. Guyane Fr. **3:** 262. 1953.

*ZYGIS AROMATICA (p. 46). Ind. Occ.; Herb. Desv., s.v. = **Satureja viminea** L.; Briquet in Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 300. 1897.

*BUCHNERA CAPILLARIS (p. 46). Guyana; Herb. Desv., s.v. = **Lindernia crustacea** (L.) F. Mueller; Philcox, Kew Bull. **18:** 310. 1965.

*DURANTA MICROPHYLLA (p. 46). Antilles; Herb. Desv., s.v. = **Duranta erecta** L. var. **domingensis** Urban, Symb. Antill. **7:** 355. 1912. *Duranta repens* L. is the generally accepted specific name when it is combined with *D. erecta* as a synonym. The varietal name has not been published with *D. repens*, to my knowledge. Urban listed *Duranta microphylla* Ham. with a question mark as a synonym of his variety and indicated that it was a later homonym of *D. microphylla* Willd. (1814).

*POARIUM VERONICOIDES (p. 46). Hispaniola; Herb. Desv., s.v. (P!) = **Stemodia parviflora** Aiton. Urban (Symb. Antill. **8:** 632. 1921) assigned the Hamilton name to synonymy with a question mark. Philcox (pers. comm.) located material in Paris and described it as a "diminutive state of *Stemodia parviflora* Ait."

*SCROPHULARIA MICRANTHA (p. 47). Hispaniola; Herb. Desv., s.v. = **Scrophularia minutiflora** Penn. Proc. Acad. Nat. Sci. Philadelphia **75:** 18. 1923. Urban (Symb. Antill. **1:** 403. 1900) had indicated that *S. micrantha* Desv. was a later homonym of the same name as used by d'Urville (1822), although later (*ibid.* **8:** 632. 1921) he accepted the Hamilton binomial without reference to d'Urville. Pennell supplied a new name and suggested that a specimen by Poiteau might be an isotype. Philcox (pers. comm.) found two sheets of a Poiteau collection in Paris, but no material attributable to Desvaux or Hamilton.

LOPHIA PHOENICEA, "nom. nov." (p. 47). Nevis, Martinique, v.v.; Herb. Desv., s.v. = **Alloplectus cristatus** (L.) Martius; Urban, Symb. Antill. **2:** 356. 1900.

*CLEOME ACULEATA (p. 48). Hispaniola; Herb. Desv., s.v. = **Cleome aculeata** L. Hamilton indicated that his binomial represented a new species and did not cite Linnaeus. Gillis could not find a specimen in Paris.

*CLEOME MICRANTHA (p. 48). Guyana; Herb. Desv., s.v. This name can not be placed.

*PASSIFLORA CYATHOPHORA (p. 48). Guyana; Herb. Desv., s.v. = **Passiflora auriculata** HBK.; Killip, Publ. Field Mus. Bot. **19:** 122. 1938. Killip (*ibid.*, p. 124) cited *Richard* (P) as the type of *P. cyathophora*.

*PASSIFLORA LANCIFOLIA (p. 48). Antilles; Herb. Desv., s.v. (P!) = **Passiflora lancifolia** Ham. Killip (Publ. Field Mus. Bot. **19:** 237, 238. 1938) accepted this as a rare species, having seen a specimen in the Desvaux Herbarium, which he stated was probably from Jamaica. Adams (Fl. Pl. Jamaica, 495. 1972) considered the species endemic to Jamaica.

*PASSIFLORA GOSSYPIFOLIA (p. 48). Herb. Desv., s.v. = **Passiflora foetida** L. var. **gossypifolia** (Desv.) Mast.; Killip (Publ. Field Mus. Bot. **19:** 484–487. 1938) cited "*Poiteau* in 1802 (B, Gen, P, type)" from the Dominican Republic and referred to the "very short indument described by Desvaux as 'tomentose.' "

*HIBISCUS ARBOREUS (p. 49). Guadeloupe, v.v.; Herb. Desv. = **Hibiscus tiliaceus** L. Hamilton cited Brown and Sloane references and plates that are usually regarded as typifying the species.

PHYMOSIA ABUTILOIDES, "comb. nov." (p. 50). Bahamas; Herb. Desv., s.v. (P!) = **Phymosia abutiloides** (L.) Ham. Fryxell (Madroño **21:** 156. 1971) credited this combination to Desvaux ex Hamilton.

*GLYCINE EMARGINATA (p. 50). Hispaniola; Herb. Desv., s.v. = **Galactia pendula** Pers. Urban (Symb. Antill. **2:** 329. 1900) gave this synonymy and may have seen a specimen. The binomial was published by Desvaux (Jour. Bot. Desvaux **3:** 78. 1814).

*NEUROCARPON GUIANENSE (p. 50). Guyana; Herb. Desv., s.v. = **Clitoria cajanifolia** Bentham in Martius, Fl. Brasil. **15**(1)**:** 121. 1859.

NEUROCARPON ELLIPTICUM (p. 51). Antilles; Herb. Desv., s.v. = **Clitoria rubiginosa** Juss. Bentham (in Martius, Fl. Brasil. **15**(1)**:** 119. 1859) referred Hamilton's name to *Clitoria glycinoides* DC., which is now regarded as a synonym of *C. rubiginosa* Juss. Desvaux published the binomial in Jour. Bot. Desvaux **3:** 75. 1814.

"*Neurocarpum rubiginosum* Ham. Prodr. (1825) p. 51" was listed by Bentham (in Martius, Fl. Brasil. **15**(1)**:** 119. 1859) and by Urban (Symb. Antill. **8:** 301. 1920), although Hamilton did not use this binomial.

*DOLICHOS CYLINDRICUS (p. 51). Guyana; Herb. Desv., s.v. = **Vigna vexillata** (L.) A. Rich.; Bentham in Martius, Fl. Brasil. **15**(1)**:** 194. 1859.

*AESCHYNOMENE CASSIOIDES (p. 51). Guyana; Herb. Desv., s.v. = **Aeschynomene histrix** Poiret. Rudd (Contr. U. S. Natl. Herb. **32:** 81. 1955), following Bentham's action, placed the Hamilton binomial in synonymy with a question mark.

*EUPATORIUM CAPILLARE (p. 51). Hispaniola; Herb. Desv., s.v. = **Brickellia diffusa** (Vahl) A. Gray; Urban, Symb. Antill. **8:** 717. 1921.

*EUPATORIUM RETICULATUM (p. 51). Jamaica; Herb. Desv., s.v. This name has not been placed. Moore (in Fawcett & Rendle, Fl. Jamaica **8:** 185. 1936) stated, "The short description is inadequate for determination," and the name is not listed by Adams (Fl. Pl. Jamaica, 1972). There are two later homonyms (Hooker & Arnott, Bot. Beechey Voy. 29. 1830, with a type from Valparaiso; and A. Richard, Fl. Cuba **2:** 39. 1853, from Cuba).

*BACCHARIS ODORATA (p. 52). Jamaica; Herb. Desv., s.v. = **Pluchea odorata** Cass.; Urban, Symb. Antill. **5:** 250. 1907.

*SPILANTHES SARMENTOSA (p. 52). Hispaniola; Herb. Desv., s.v. = **Spilanthes sarmentosa** Ham. Urban (Symb. Antill. **8:** 734. 1921) listed this binomial as a "species dubia." Gillis was unable to find a specimen in Paris, and current students of the genus have been unable to locate material or to place the name.

*ELEPHANTOPUS VIRGATUS (p. 52). Guyana; Herb. Desv., s.v. This name has not been placed, and no material has been located by specialists on the genus.

*CYRTOPODIUM ELEGANS (p. 53). Antigua, v.v. = **Tetramicra canaliculata** (Aublet) Fedde. Garay and Sweet (in Howard, Fl. Lesser Antilles **1:** 162. 1974) reported the Hamilton type to be from Green Castle, Antigua, with a collection preserved in Paris.

*EPIDENDRUM CUSPIDATUM (p. 53). Nevis, Carribeis, v.v.; "Ic. pict. v" = **Epidendrum ciliare** L. Garay and Sweet (in Howard, Fl. Lesser Antilles **1:** 128. 1974) state that no specimen was preserved. The type of the Loddiges material that Hamilton cited is a plate in *The Botanical Cabinet* (**1:** *pl. 10.* 1817). The plant was originally from Dominica. Hamilton's reference to living material is unexplained, although the reference to "Ic. pict. v" may be to the Loddiges plate. Gillis, however, found a specimen in the Desvaux herbarium marked *Epidendrum ciliare* in Desvaux's handwriting.

*MAPROUNIA GLAUCA (p. 54). Guyana; Herb. Desv., s.v. Hamilton credited Aublet with the generic name, which had originally been published as *Maprounea* Aublet.

*BEGONIA SUAVEOLENS (p. 54). Antilles; Herb. Desv., s.v. = **Begonia purpurea** Sw. Schulz (in Urban, Symb. Antill. **7:** 17. 1911) placed the Hamilton binomial in synonymy and used the expression "probabiliter." *Begonia purpurea* Sw. is regarded as endemic to Jamaica.

*CALADIUM VIOLACEUM (p. 54). Ind. Occ.; Herb. Desv., s.v. = **Colocasia esculenta**

(L.) Schott. Hamilton referred to Desfontaines's "Cat. Hort. Paris." in his description. Such material was regarded by De Candolle (Monogr. Phanerog. **2:** 492. 1879) as *C. antiquorum*.

*CROTON MICROCARPUS (p. 55). Hispaniola; Herb. Desv., s.v. (P!) = **Croton microcarpus** Ham. Urban (Symb. Antill. **3:** 292. 1903) stated that the species could not be determined, but in a later volume (*ibid*. **8:** 257. 1920) he accepted the name. Gillis found a specimen marked in Desvaux's hand. The Hamilton binomial was not listed in *Index Kewensis*, and *Croton microcarpus* Mueller-Arg. (in Martius, Fl. Brasil. **11**(2)**:** 142. 1873) is a later homonym for a Brazilian species.

*CROTON GUADELOUPENSIS (p. 55). Guadeloupe; Herb. Desv., s.v. = **Croton astroites** Aiton. Urban (Symb. Antill. **3:** 292. 1903) established the synonymy. The binomial was not listed in *Index Kewensis*.

CROTON DICHOTOMUS (p. 55). Hispaniola = **Adelia bernardia** L. Hamilton made this observation.

*CROTON BAHAMENSIS (p. 55). Bahamas; Herb. Desv., s.v. (P!) = **Croton lucidus** L. Urban (Symb. Antill. **3:** 292. 1903) suggested the proper identification. Gillis found a specimen in Paris. The binomial was not listed in *Index Kewensis*. As a consequence, *C. bahamensis* Millsp. (Publ. Field Mus. Bot. **2:** 308. 1909) is a later homonym, and Gillis concluded that this is *C. humilis* L.

CROTON PRUNIFOLIUS (p. 55). Hispaniola, Jamaica; Herb. Desv., s.v. = **Croton glabellus** L. Urban (Symb. Antill. **8:** 351. 1920) credited Geisel with the synonymy.

CROTON ELEUTERIA (p. 56). Jamaica; s.v. = **Croton eluteria** (L.) Sw. The correct nomenclature of *Clutia eleuteria* L. remains an unsolved problem.

*CROTON MICROSTACHYUS (p. 56). Hispaniola; Herb. Desv., s.v. (P!) = **Croton microstachyus** Ham. Urban (Symb. Antill. **8:** 351. 1920) accepted this species and noted that a specimen was in Paris. The binomial was not included in *Index Kewensis*, and Gillis noted that *Croton microstachyum* Baillon (Adansonia **4:** 366. 1863) from Brazil was a later homonym.

Gillis (1978) noted that *Croton gonaivensis* Urban is a synonym.

*CROTON ANGUSTIFOLIUS (p. 56). Hispaniola; Herb. Desv., s.v. Urban (Symb. Antill. **3:** 292. 1900) stated that the description was too brief to permit identification. Later (*ibid*. **8:** 357. 1920) he noted a similarity to *C. megaladeni* Urban but listed *C. angustifolius* in a group of species not placed satisfactorily. Moscoso (Catal. Fl. Doming. 305. 1943) listed the species as endemic but failed to cite additional material.

*TOBINIA CORIACEA (p. 57). Jamaica; Herb. Desv., s.v. = **Zanthoxylum spinosum** (L.) Sw.; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 178. 1920.

TOBINIA SPINOSA, "comb. nov." (p. 57). Jamaica = **Zanthoxylum spinosum** (L.) Sw.; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 178. 1920.

TOBINIA ACUMINATA, "comb. nov." (p. 57). Jamaica = **Zanthoxylum acuminatum** Sw.; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 179. 1920.

TOBINIA EMARGINATA, "comb. nov." (p. 57). Jamaica = **Zanthoxylum spinosum** (L.) Sw.; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 178. 1920.

TOBINIA TERNATA, "comb. nov." (p. 57). Dominica = **Zanthoxylum punctatum** Vahl; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 177. 1920.

*SMILAX FLAVESCENS (p. 58). Guyana, Hispaniola; Herb. Desv., s.v. = **Smilax papyracea** Duhamel; Schulz in Urban, Symb. Antill. **8:** 99. 1920.

*SMILAX FLORIBUNDA (p. 58). Guyana; Herb. Desv., s.v. = **Smilax cuspidata** Michaux. This reference was suggested in *Index Kewensis* and can not be verified. No material has been found.

*SMILAX ELLIPTICA (p. 58). Ind. Occ.; Herb. Desv., s.v. = **Smilax zeylanica** L. Schulz (in Urban, Symb. Antill. **5:** 47. 1904) stated that this was surely not a native plant.

*SMILAX ILICIFOLIA (p. 58). Antilles; Herb. Desv., s.v. = **Smilax coriacea** Sprengel var. **ilicifolia** (Ham.) Schulz in Urban, Symb. Antill. **8:** 99. 1920. Schulz indicated that there was a specimen in the Desvaux herbarium.

*SMILAX SAGITTATA (p. 58). Ind. Occ.; Herb. Desv., s.v. = **Smilax aspera** L. Schulz (in Urban, Symb. Antill. **5:** 47. 1904) reported that the designation of this specimen from India Occidentale was an error for India Orientale, and that the plant was *Smilax aspera* as A. de Candolle had indicated (Monogr. Phanerog. **1:** 165. 1878).

*SMILAX RETICULATA (p. 58). Ind. Occ.; Herb. Desv., s.v. = **Smilax lanceolata** L.; Howard, Taxon **28:** 57. 1979.

*ACACIA STENOSTACHYA (p. 59). Guyana; Herb. Desv., s.v. = **Piptadenia psilostachya** (A. DC.) Bentham, Trans. Linn. Soc. London **30:** 372. 1875.

*ACACIA HAMILTONII (p. 59). Jamaica; Herb. Desv., s.v. = **Calliandra portoricensis** (Jacq.) Bentham; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 142. 1920.

*ACACIA LINEARIS (p. 59). Jamaica; Herb. Desv., s.v. = **Calliandra portoricensis** (Jacq.) Bentham; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 142. 1920. *Acacia linearis* Ham. is a later homonym of Sims (Curtis's Bot. Mag. **47:** *t. 2156.* 1820).

*ACACIA UNGULATA (p. 59). Jamaica; Herb. Desv., s.v. = **Calliandra portoricensis** (Jacq.) Bentham; Fawcett & Rendle, Fl. Jamaica **4**(2)**:** 142. 1920.

ACACIA HUMBOLDTII, "nom. nov." (p. 60). Guyana = **Acacia lutea** Hitchc. Bentham (Trans. Linn. Soc. London **40:** 500. 1875) referred the Hamilton name to *Acacia macracantha* Humb. & Bonpl. ex Willd., which Fawcett and Rendle (Fl. Jamaica **4**(2)**:** 138. 1920) referred to *A. lutea* Hitchc.

*ACACIA MICRANTHA (p. 60). Guyana; Herb. Desv., s.v. = **Pithecellobium parvifolium** Bentham; Bentham in Martius, Fl. Brasil. **15**(2)**:** 454. 1876. *Acacia micrantha* Bentham (Trans. Linn. Soc. London **30:** 526. 1875) from Mexico is a later homonym, and the plant has been renamed *Acacia parviflora* Little (Phytologia **6:** 506. 1959).

*ACACIA SELENICARPA (p. 60). Guyana; Herb. Desv., s.v. = **Acacia albida** Delile. Bentham (Trans. Linn. Soc. London **30:** 515. 1875) established the

synonymy and noted "patria falsa."

*INGA CAPITATA (p. 61). Guyana; Herb. Desv., s.v. = **Inga capitata** Desv. Jour. Bot. Desvaux **3:** 71. 1814. Lemée (Fl. Guyane Fr. **2:** 43. 1952) accepted this species.

INGA CORNIGERA, "comb. nov." (p. 61). Carthagena, Cuba = **Acacia cornigera** (L.) Willd.; Janzen, Smithson. Contr. Bot. **13:** 80. 1974. Hamilton cited references to *Acacia cornigera* Hort. Kew. and *Mimosa cornigera* Jacq. The species is known today from Mexico and Central America.

INGA SPINIFOLIA (p. 61). Ind. Occ.; s.v. = **Pithecellobium circinale** (L.) Bentham; Bentham, Trans. Linn. Soc. London **30:** 573. 1875. The binomial was published by Desvaux (Jour. Bot. Desvaux **3:** 72. 1814).

*INGA FAECULIFERA (p. 61). Hispaniola, Santo Domingo; Herb. Desv., s.v. = **Parkia africana** R. Br.; Burkart, Jour. Arnold Arb. **57:** 524. 1976. Gillis was unable to find specimens under *Inga, Prosopis faeculifera* Desv. (Ann. Sci. Nat. **9:** 426. 1826), or *Parkia*.

*FICUS GUIANENSIS (p. 62). Guyana; Herb. Desv. = **Ficus guianensis** Ham. Lemée (Fl. Guyane Fr. **1:** 508. 1955) listed this species but was unable to place it.

HAMILTON'S BIBLIOGRAPHY

Hamilton (1832–1835) referred to his first publication as a "small Medical Work (now I believe out of print)" that was published shortly after his graduation in 1808. No exact title or reference to this has been found. Following the publication of the *Prodromus* in 1825, Hamilton wrote a number of letters to the *Gardener's Magazine* between 1826 and 1836. Many of these are based on his notes on his experiences in the West Indies. While he was there, Hamilton received seeds from many sources; he distributed these through the West Indies and returned some to Europe (cf. *Ocimum montanum*, Curtis's Bot. Mag. **57:** *t. 2996*. 1830). Among his correspondents were E. N. Bancroft and J. MacFadyen (Jamaica), Sir Robert Kerr Porter (Venezuela), Thomas Higson and Edward Watts (Carthagena, Colombia), and D. C. Lansereur, the elder (Rennes, France). Hamilton described his goal as follows: "May we hope that the reformed system [of plant cultivation] which has at last happily commenced, will bring with it better things; awaken the planters, so long slumbering on the verge of ruin, to a sense of their true interests and convert the West Indian islands, from a fatal millstone about the neck of Great Britain, into what a bountiful providence designed they should be, a terrestrial paradise, and a source of benefit to the parent state. This is a consummation I have incessantly laboured to effect, by calling the attention of those most interested to the true capabilities of those mismanaged and comparatively mismanaged regions. . . ." Hamilton took credit for introducing *Caesalpinia coriaria*, the divi-divi tree, to Barbuda; and his description of *Psophocarpus tetragonolobus* (under *Dolichos*), the winged bean, may well be the earliest record of the plant in the New World.

After a hiatus in his writing from 1838 to 1844, Hamilton began an equally

concentrated contribution to the *Pharmaceutical Journal*. An obituary notice in that journal in 1856 referred to him as "our valued correspondent." With further study Hamilton's obscure and formerly unindexed letters can serve to date plant introductions and to detail the medicinal uses of local plants during a period when literature on the West Indies tends to be scanty.

In the following listing the letters that appear without titles in journals are abstracted to subject matter. One letter on the subject of the medicinal properties of *Piscidia* was stated to be in Volume 33, page 45, of "Mr. Nicholson's Journal"—a reference that can not be located.

1814

Some particulars respecting hail storms in the West Indies in the month of April 1814; and experiments to ascertain the medicinal powers of the *Hura crepitans*. Tilloch Philos. Mag. **44:** 191–193 (not seen).

1825

Prodromus plantarum Indiae Occidentalis. xvi + 67 pp. Treuttel & Würtz, London.

1826

Cultivation of *Myrica carolinensis*. Gardener's Mag. **1:** 403.

1828

Culture of *Hypanthera moringa* in the West Indies. Gardener's Mag. **3:** 157.
Letter: Report on Arracacha plant. Gardener's Mag. **3:** 352.
Letter: Arracacha, *Brownea coccinea* and el achira. Gardener's Mag. **4:** 157, 158.
Letter: The pita plant. Gardener's Mag. **4:** 161.
Letter: The duffin bean. Gardener's Mag. **4:** 190.
Letter: Charcoal powder for packing plants to be transported. Gardener's Mag. **4:** 190.
Letter: List of plants introduced from Carthagena. Gardener's Mag. **4:** 278.
Letter: Report on the arracacha plant. Gardener's Mag. **4:** 402.
Letter: The cow cabbage. Gardener's Mag. **4:** 403.
Letter: Annuals vs. perennials. Gardener's Mag. **4:** 442.
Letter: Timber to use in building hot houses. Gardener's Mag. **4:** 442.
Letter: The locust tree. Gardener's Mag. **4:** 443.
Letter: Winter's rest to extra-tropical plants. Gardener's Mag. **4:** 443.
Letter: List of plants introduced from Carthagena. Gardener's Mag. **4:** 443.
Letter: *Psidium cattleyanum*. Gardener's Mag. **4:** 448.
Letter: *Myrica cerifera*. Gardener's Mag. **4:** 448.

1829

List of timber trees in the province of Chocó, Colombia. Gardener's Mag. **5:** 44–47.
Letter: Vines within the tropics. Gardener's Mag. **5:** 98–100.

1830

Letter: *Argemone mexicana*. Gardener's Mag. **6:** 315.

Letter: *Dolichos tetragonolobus*. Gardener's Mag. **6:** 315.
Letter: Meloncito d'olor, *Cucumis* sp. Gardener's Mag. **6:** 315.
Letter: Seeds from Carthagena. Gardener's Mag. **6:** 493.

1831

Letter: Kassaba melon. Gardener's Mag. **7:** 101.
Letter: A new species of *Canna*. Gardener's Mag. **7:** 226.
Letter: The genus *Georgia*. Gardener's Mag. **7:** 716.

1832

Letter: *Caesalpinia coriaria*. Gardener's Mag. **8:** 46, 47.
Letter: Choco palms. Gardener's Mag. **8:** 79, 80.
Letter: Enquiry about a flax or hemp machine. Gardener's Mag. **8:** 96.
Letter: The pita de guataca . . . for cordage. Gardener's Mag. **8:** 240–242.
Letter: Enquiry about dissolving India rubber. Gardener's Mag. **8:** 735.
Letter: *Tacca pinnatifida*. Gardener's Mag. **8:** 736.

1833

Letter: *Oxalis brasiliensis*. Gardener's Mag. **9:** 618.

1834

Letter: Uvedale's St. Germain pear. Gardener's Mag. **10:** 61.
Letter: Apio roots from Caracas. Gardener's Mag. **10:** 296.
Letter: Germination experiment. Gardener's Mag. **10:** 368.
Letter: Plants sent from Caracas. Gardener's Mag. **10:** 396.
Letter: *Caesalpinia coriaria* and *Cassia fistula*. Gardener's Mag. **10:** 404, 405.
Letter: *Bignonia ophthalmica* and *Oxalis crenata*. Gardener's Mag. **10:** 453.
Letter: Victoria wheat and yucca starch. Gardener's Mag. **10:** 454, 455.
Letter: The shaddock and mango. Gardener's Mag. **10:** 576, 577.
On the medical properties of the *Piscidia erythrium* or Jamaica dogwood. Trans. Roy. Med.-Bot. Soc. London **3:** 17–22.
Some account of the febrifuge bark of a tree called el malambo, the produce of South America. Trans. Roy. Med.-Bot. Soc. London **3:** 67–77.

1836

Letter: The palo de vaca or cow tree. Gardener's Mag. **12:** 100–103.
Letter: The genus *Bambusa*. Gardener's Mag. **12:** 197, 198.
Letter: Timber trees of Caracas. Gardener's Mag. **12:** 210, 211.
Letter: Cultivating wheat, etc. in the West Indies. Gardener's Mag. **12:** 211–213.

1837

American sumach; to chemists, dyers, tanners and others. Agr. Hort. Soc. India Trans. **3:** 92–94 (not seen).
On the American sumach. Madras Jour. Lit. Sci. **15:** 363–365 (not seen).

1838

Letter: The cow tree (*Galactodendron speciosum*). Gardener's Mag. **14:** 495.

1844

Sur les propriétés narcotiques de l'écorce de la racine de *Piscidia erythrina*. Jour. Pharm. Chim. III. **6:** 422, 423.

1845

On the Jamaica dog-wood. Pharm. Jour. **4:** 76–78, 111–114.

On the medicinal properties of the *Argemone mexicana* and *Hura crepitans*. Pharm. Jour. **4:** 167–170.

Over de narcotische eigenschappen van den bast des wortels van *Piscidia erythrina* Jacq. "Tijdschr. Schei. Artsenijh." **2:** 111–113 (not seen).

1846

On the *Argemone mexicana, Hura crepitans, Jatropha curcas* and *J. multifida*. Pharm. Jour. **5:** 23–27.

On the genus *Jatropha*, and the *Janipha manihot* and *loeflingii*. Pharm. Jour. **5:** 27–33.

Medical properties of the *Fevillea cordifolia*. Pharm. Jour. **5:** 33–35.

On the *Moringa pterygospermum* or oil of ben tree and its uses, economical and officinal. Pharm. Jour. **5:** 58, 59.

On the gum of the *Rhus metopium* and on the *Aristolochia odoratissima, trilobata* and *anguicida*. Pharm. Jour. **5:** 60, 61.

On the properties ascribed to some species of *Comocladia*. Pharm. Jour. **5:** 114–117.

On the properties of some species of *Cathartocarpus*. Pharm. Jour. **5:** 118–121.

On the medical and economical properties of *Anacardium occidentale* or cashew nut tree. Pharm. Jour. **5:** 268–273.

On the medicinal properties of the species of *Cassia* found in the West Indies. Pharm. Jour. **5:** 345–351.

On the properties of the *Hippomane mancinella* or manchineel tree. Pharm. Jour. **5:** 408–412.

On the medical and commercial properties of *Caesalpinia coriaria* or divi-divi. Pharm. Jour. **5:** 443–452.

Om gummi af *Rhus metopium* og om *Aristolochia odoratissima, trilobata*, og *anguicida* samt *Moringa pterygospermum*. Arch. Pharm. Kjøbenhavn **3:** 413–415 (not seen).

1847

On the medical and economical properties of *Rhizophora mangle* or mangrove tree. Pharm. Jour. **6:** 11, 12.

On the noxious properties of the *Echites suberecta*, or savanna flower, and their antidotes. Pharm. Jour. **6:** 23, 24.

On the *Maranta arundinacea* and its application as an antidote to animal and vegetable poisons. Pharm. Jour. **6:** 25–28.

On the reputed properties of some of the species of *Cleome*. Pharm. Jour. **6:** 79, 80.

On the *Capparis cynophallophora* or bottle cod. Pharm. Jour. **6:** 81, 82.

On the properties of the *Asclepias curassavica*, or bastard ipecacuanha. Pharm. Jour. **6:** 212–216.

On the *Muracuja ocellata* or West Indian opium. Pharm. Jour. **6:** 216, 217.
On the malanbo bark of the province of Carthagena, S. America. Pharm. Jour. **6:** 255–259.
On some properties of the genus *Amyris* which are little known. Pharm. Jour. **6:** 322–326.
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On the properties of the *Bocconia frutescens* and *Clusia*. Pharm. Jour. **6:** 581–584.
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Bemerkungen über *Bocconia frutescens*. Allg. Gartenzeit. **15:** 375, 376.

1848

On the *Canna achira*, or tous-les-mois. Pharm. Jour. **7:** 56–60.
On the medical and economical properties of the *Sapindus saponaria*, soap-berry or black nickar tree. Pharm. Jour. **7:** 225–230.
Some further particulars respecting the *Rhus metopium* or hog-gum tree. Pharm. Jour. **7:** 270–277.

1849

A few statistics of cholera at Plymouth. Pharm. Jour. **8:** 168, 169.
Un nouveau poison. Jour. Pharm. Chim. III. **15:** 123.

1850

On the purgative properties of the oils obtained from the plants indigenous to the Antilles. Pharm. Jour. **9:** 129–131.
On the ava root of the Sandwich Islands. Pharm. Jour. **9:** 218–220.

1851

On the cultivation, preparation and properties of the *Myrica cerifera*, and *M. carolinensis*, or waxtree of Carolina. Pharm. Jour. **10:** 450–454.

1853

Observations on the late earthquake in the west of England. Pharm. Jour. **12:** 181–183, 308, 309.
On the oil of *Argemone mexicana* as a remedy for Asiatic cholera. Pharm. Jour. **12:** 292, 293.
Queries respecting the poisonous properties of fish. Pharm. Jour. **12:** 344.
Some notices of the hurricane at Plymouth, England, of 1824. Pharm. Jour. **12:** 388, 389.

1854

On the medicinal properties of the *Coffea arabica*. Pharm. Jour. **13:** 329, 330.
A few observations on the use of *Argemone mexicana* in cholera. Pharm. Jour. **13:** 642.

1855

The metal aluminium, its probable use in pharmacy. Pharm. Jour. **14:** 16–18.
Use of mushrooms in Russia. Pharm. Jour. **14:** 66, 67.

1856

On the nutritive properties of the mass which remains after the expression of the nuts of the cocoa, etc. Pharm. Jour. **15:** 350.
Notes on the materia medica of the Paris Exhibition. Pharm. Jour. **15:** 410, 411.

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NEW CENTRAL AMERICAN TAXA OF HELICONIA (HELICONIACEAE)

W. JOHN KRESS

MEMBERS OF THE primarily neotropical genus *Heliconia* L. (Heliconiaceae) are medium to large, sometimes treelike, herbaceous plants with colorful, often stout inflorescences. Although usually quite common in the neotropics, they are not often collected because of their large, fleshy stature. The recent taxonomic treatment of the heliconias of Costa Rica (Daniels & Stiles, 1979) emphasizes the need for critical field observations and photographs of live specimens *in situ*. Indispensable diagnostic characters, such as orientation of the inflorescence (erect vs. pendent), arrangement of the cincinnal bracts (spiral vs. distichous), color of various reproductive structures, and certain vegetative features, are in most cases absent from dried herbarium collections and are not recorded by the collector. R. R. Smith (1968) recognized 38 species in his unpublished revision of the heliconias of Middle America, which was based largely on herbarium material. Daniels and Stiles (1979) have listed at least that many species from only one of the countries covered in Smith's work. Even despite possible differences in species concepts and the fact that Costa Rica is floristically rich, the disparity between the two treatments in the number of described species of *Heliconia* is striking. As good field descriptions of living plants become available, additional new taxa of this genus will certainly be recognized.

The five new species and three new varieties of *Heliconia* treated here have been described from living collections in their natural habitats. Seven of the newly recognized taxa are from Panama, while the eighth, a variety previously recognized but not validly published, is found in Guatemala and El Salvador. These descriptions are part of a larger revision of the Central American species of *Heliconia* with pendent inflorescences (Kress, in prep.).

Descriptive terminology for the most part follows that of Daniels and Stiles (1979). Their "branch bracts" are referred to here as cincinnal bracts, and the basal width of these is measured from margin to margin near the rachis. Although other workers on Central American heliconias have made general reference to the single reduced staminode of the flowers, this floral part is used as a specific character in the following descriptions. The fruits have been described variously as berries, capsules, and "schizocarpic berries." An early study by Humphrey (1896) on seed development in the Zingiberales demonstrated that the mature fruit of *Heliconia* is a drupe with a stony endocarp enclosing the true seed. This interpretation is accepted here.

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Heliconia maculata Kress, sp. nov. FIGURE 1.

Planta herbacea 2–2.5 m. alta; caulis subviridi-griseus maculatus; inflorescentia pendens; pedunculus viridis et marroninus, glaber; rhachis rubra, glabra vel puberula; cincinnorum bracteae spirales, basi rubrae, ad apicem viridescentes, glabrae; perianthium basi luteum, apice viridulum, glabrum vel puberulum; ovarium album, pubescens; fructus lazulinus, glaber vel puberulus.

TYPE: Panama, Colón, along Río Guanche, 1 km. from the road to Portobelo, elev. ca. 8 m., 27 August 1980, *Kress & Knapp 80-1240* (DUKE, holotype; F, GH, K, MO, PMA, isotypes).

Herb with *Musa*-like habit, 2–2.5 meters tall. Leafy shoots congested in groups of 3 to 25; pseudostem pale greenish gray with distinctive dark brown spots throughout, glabrous, 1.2–1.7 meters tall, 2.2–2.5 cm. in diameter; leaves 6 per shoot, blades all tending to lie in single plane; petiole olive green, glabrous, 22–34 cm. long, 8–10 mm. in diameter; blade widest toward acute apex, base unequal and attenuate, extending along petiole, the upper surface green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow and glabrous to slightly scurfy, the longest blade 1.1–1.3 meters long, 24–26 cm. wide. Inflorescence pendent, to 51 cm. long (excluding peduncle); peduncle green and dark maroon, glabrous, 7–32 cm. long, 1 cm. in diameter; rachis flexuose, dull red, glabrous to slightly puberulous, 7–8 mm. in diameter at base; cincinnal bracts spirally arranged, 7 or 8 per inflorescence, oriented 90° to axis of inflorescence, the basal bract fertile or sterile, the middle bract with apex acuminate, margins straight becoming somewhat flared at base, inner surface pale orange and glabrous, outer surface red basally becoming green toward apex and glabrous, 14–17 cm. long, 4–4.5 cm. wide at base. Floral bracts translucent at anthesis, quickly decomposing, cream, glabrous to puberulous abaxially, glabrous adaxially, 4–5 cm. long, 1.1–1.4 cm. wide at base. Flowers 15 to 20 per cincinnus; pedicel pale yellow, pubescent to hirsute, 1–1.5 cm. long; perianth yellow basally becoming greenish toward apex, glabrous to slightly puberulous, 5 cm. long, 1 cm. wide at base, at anthesis curved 30–50°; free sepal lowermost, slightly reflexed, fused sepals with apices not reflexed; staminode white, apex apiculate, 7–10 mm. long, 3 mm. wide; stamens with anthers flared outside perianth apex; ovary white, pubescent, 4–5 mm. long, 6 mm. wide. Drupes blue, glabrous to puberulous, 8 mm. long, 9 mm. wide; stones 6 mm. long, 5 mm. wide.

SPECIMENS EXAMINED. **Panama.** COLÓN: Río Guanche, forest, elev. ca. 50 ft., *Maas et al. 1583* (F, MO); in forest 3–7 km. from bridge, elev. 300–700 ft., *Hammel et al. 4899* (MO).

PHENOLOGY. Flowering from late July through early October.

HABITAT AND DISTRIBUTION. This species occurs naturally at lower elevations along stream banks and in adjacent understory of primary forest. It will invade more open areas (often created by man), where it generally produces

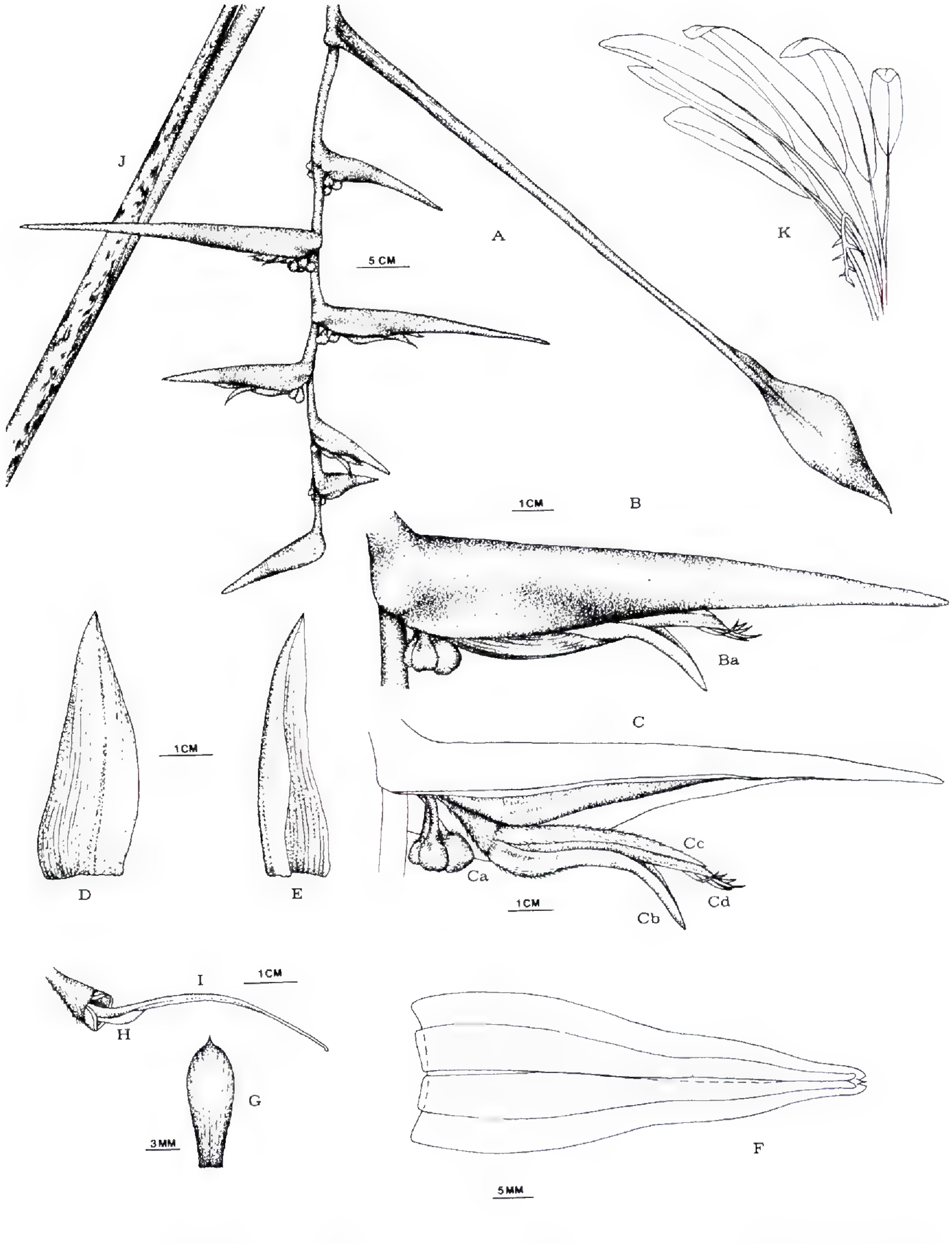

FIGURE 1. **Heliconia maculata.** A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, not reflexed; Cd, anthers, exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing two sepals fused to partially spread-open corolla tube. G, H, staminodes: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, pseudostem. K, vegetative habit.

more shoots per clump. So far *Heliconia maculata* has been collected only along Río Gaunche in Colón, Panama; it will probably also be found in other forested areas in the Atlantic coastal forests of Panama.

RELATIONSHIPS. Vegetative characters, including leaf blades that are oriented in a single plane and that are widest at the apex, and the distinctive pubescent ovaries, ally this species with *Heliconia colgantea* R. R. Smith ex Daniels & Stiles and *H. trichocarpa* Daniels & Stiles, of Costa Rica and Panama. However, it differs from these species in its spotted pseudostem (also present in *H. necrobracteata* Kress), red and green cincinnal bracts, and yellow and green perianth.

NAME. *Heliconia maculata* is named for the distinctive spotted pseudostem, which allows the plant to be identified even if it is not in flower.

Heliconia magnifica Kress, sp. nov. FIGURE 2.

Planta herbacea 4–6 m. alta; inflorescentia pendens; pedunculus et rhachis atrovinosa, pubescentia lanata aurea praedita; cincinnorum bracteae spirales, rubrae, pubescentes vel velutinae; perianthium basi album, apice lutescens pubescentia aurea praedita; ovarium album, glabrum.

TYPE: Panama, Panamá, Cerro Campana, beyond the Su Lin Motel, elev. 1000 meters, 15 August 1977, *Kress, Clarkson, & McDade 77-850* (DUKE, holotype; K, MO, isotypes).

Herb with *Musa*-like habit, 4–6 meters tall. Leafy shoots in groups of 1 to 5; pseudostem rusty brown, scurfy, 1.1–2.3 meters tall, 3–7 cm. in diameter; leaves 3 or 4 per shoot; longest petiole light green and maroon, glabrous, 1.1–1.8 meters long, 1–1.9 cm. in diameter; blade splitting into narrow lateral segments with age, base unequal and truncate to cordate, apex acute, the upper surface dark green, glabrous, with midrib yellow-green and glabrous, the lower surface green with maroon margins, glabrous, with midrib yellow-green and glabrous, the longest blade 1.1–1.9 meters long, 36–55 cm. wide. Inflorescence pendent, to 94 cm. long (excluding peduncle); peduncle dark red to burgundy, woolly with golden hairs, 30–50 cm. long, 1–1.7 cm. in diameter; rachis flexuose, red to burgundy, woolly, 1–1.6 cm. in diameter near basal bract; cincinnal bracts spirally arranged, up to 35 per inflorescence, oriented 30–50° to axis of infloresence, the basal bract usually fertile, the middle bract with apex acuminate, margins straight becoming involute at base, inner surface white to red and pubescent to velutinous, outer surface red to burgundy and velutinous to villous with golden hairs, 8–10 cm. long, 7.5–9.5 cm. wide at base. Floral bracts opaque, persistent, pink, glabrous to velutinous abaxially, glabrous adaxially, 3.5–5 cm. long, 1–1.5 cm. wide at base. Flowers 10 to 15 per cincinnus; pedicel white becoming pink near ovary, glabrous, 1–1.3 cm. long; perianth white basally becoming yellow toward apex, glabrous basally becoming tomentose with golden hairs toward apex, 5.5–6 cm. long, 1–1.2 cm. wide at base, at anthesis curved 80–90°; free sepal lowermost, reflexed, fused sepals with apices slightly

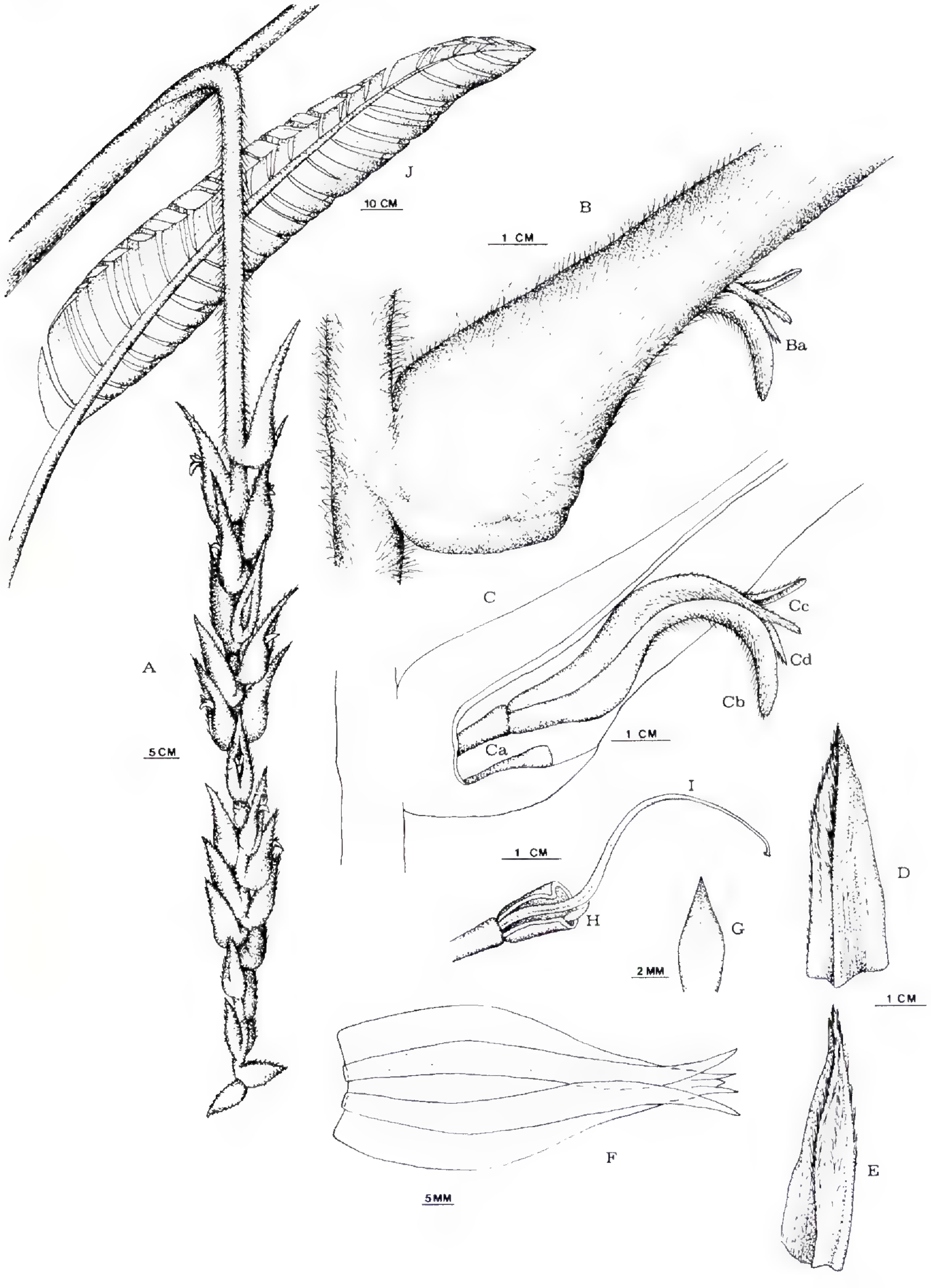

FIGURE 2. **Heliconia magnifica.** A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, partially reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing two sepals fused to partially spread-open corolla tube. G, H, staminodes: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, mature leaf, blade split into lateral segments.

reflexed; staminode white becoming yellow at acuminate apex, 5–6 mm. long, 2–3 mm. wide; stamens with anthers connivent inside apex of corolla tube; ovary white, glabrous, 1–1.1 cm. long, 5–6 mm. wide. Drupe deep blue, glabrous, 1.2–1.3 cm. long, 8–10 mm. wide; stones 9 mm. long, 6 mm. wide.

SPECIMENS EXAMINED. **Panama.** PANAMÁ. Cerro Campana: elev. 600 m., *Antonio 1250* (MO), *Antonio 1725* (MO); elev. 850 m., *Busey 847* (MO), *Liesner 627* (F, MO, NY); elev. 2600–2800 ft., *Lewis et al. 1903* (MO); elev. 800–1000 m., *Gentry 4955* (F, MO, SCZ); elev. 1000 m., *Allen 2425* (MO); near summit, elev. 1000 m., *Kress & Cooper-Smith 76-648* (DUKE); elev. 2700–3200 ft., *Hammel 3783* (MO); elev. 3300 ft., *Kress 80-1246* (DUKE); 3/4 of way to summit from Pan American Hwy., *Dwyer et al. 4850* (MO); cloud forest, *Luteyn & Kennedy 1814* (DUKE); without further location, *C. E. Smith & H. M. Smith 3399* (US).

PHENOLOGY. Flowering mainly from March to September, but mature inflorescences can be found throughout the year.

HABITAT AND DISTRIBUTION. This species is found at middle elevations (above 600 m.) in the understory of cloud forest; it is endemic to Cerro Campana in Panama.

RELATIONSHIPS. *Heliconia magnifica* is closely related to species of the pogonantha group with large pendent inflorescences, including *H. vellerigera* Poeppig, *H. ramonensis* Daniels & Stiles, and *H. xanthovillosa* Kress, all found in Central America. It is distinguished from these species by the dark red to burgundy color of the inflorescence and by the golden, woolly pubescence covering the peduncle, rachis, and cincinnal bracts.

NAME. The epithet "magnifica" has been used for this taxon for over 25 years (first by C. V. Morton, then by I. Lane,[1] and finally by R. R. Smith) but has never been validly published. Since investigators have continued to recognize the species under that name, it is used here as an adequate descriptive epithet for this "magnificent" *Heliconia.*

Heliconia necrobracteata Kress, sp. nov. FIGURE 3.

Planta herbacea 4–4.5 m. alta; caulis viridi-griseus maculatus; inflorescentia pendens, rubra; cincinnorum bracteae spirales, post anthesin celeriter marcescentes; perianthium luteum; ovarium luteum, glabrum; fructus lazulinus.

TYPE: Panama, Coclé, 6 miles beyond El Valle de Antón behind Cerro Gaital, elev. 900 meters, 12 August 1977, *Kress, Clarkson, & McDade 77-842* (DUKE, holotype; K, MO, isotypes).

Herb with *Musa*-like habit, 4–4.5 meters tall. Leafy shoots in groups of 3 to 12; pseudostem dull grayish green with brown spots, glabrous, 1–2 meters tall, 4–6.5 cm. in diameter; leaves 3 to 5 per shoot; longest petiole olive

[1]References throughout this paper to I. Lane refer to annotations made by Lane on herbarium specimens.

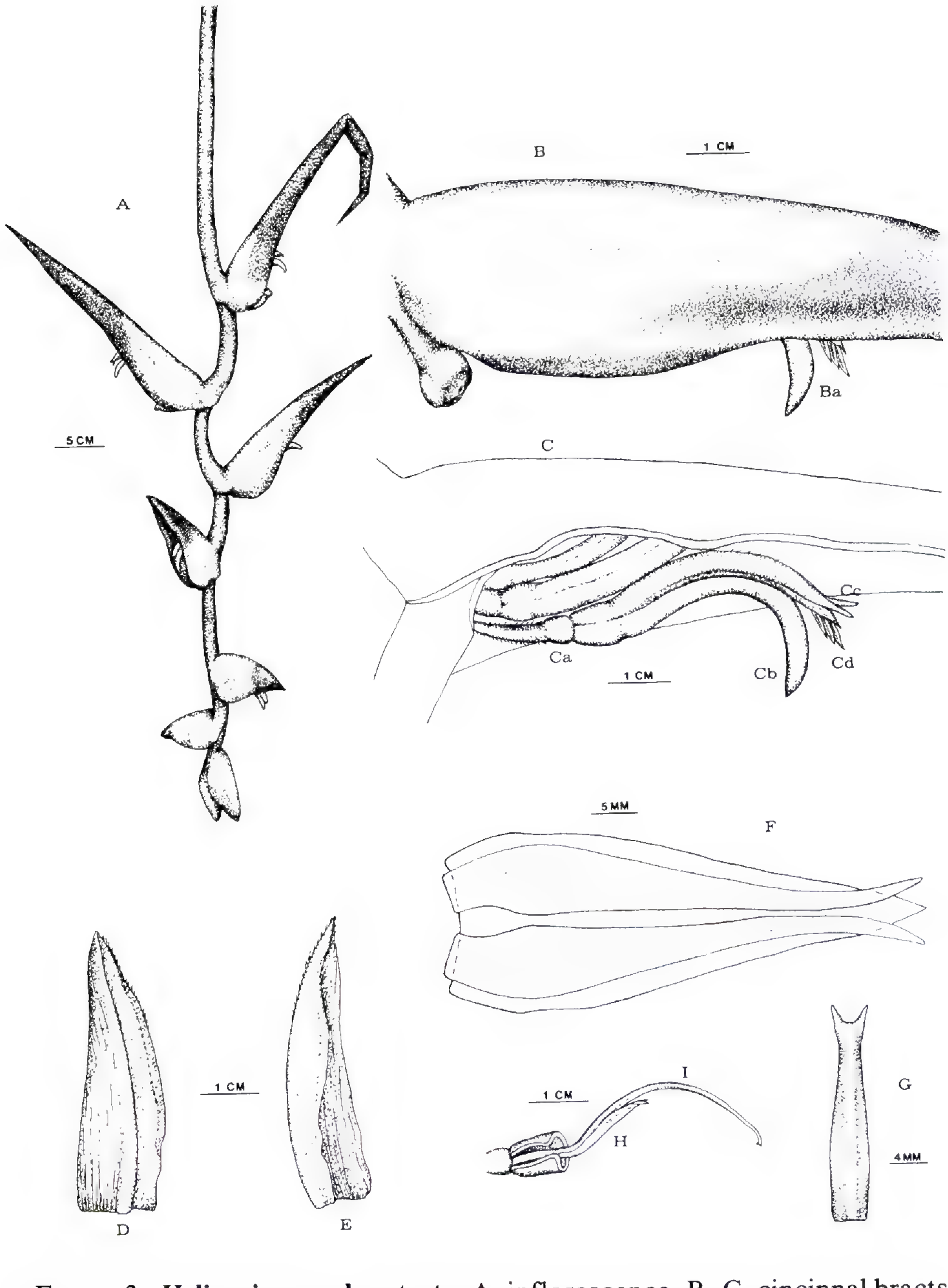

FIGURE 3. **Heliconia necrobracteata.** A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, partially exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing two sepals fused to partially spread-open corolla tube. G, H, staminodes: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

green, glabrous, 65–100 cm. long, 1.5–2 cm. in diameter; blade widest toward acute to obtuse apex, with base unequal and attenuate along petiole, the upper surface dark green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.4 meters long, 25–35 cm. wide. Inflorescence pendent, 40–55 cm. long (excluding peduncle); peduncle red, glabrous to puberulous, 25–35 cm. long, 1.3–1.8 cm. in diameter; rachis flexuose, dark red, puberulous, 1–1.4 cm. in diameter at base; cincinnal bracts spirally arranged, 10 to 22 per inflorescence, oriented 40–45° to axis of inflorescence, becoming more reflexed with age, the basal bract usually fertile, the middle bract with apex acuminate, margins straight, inner surface yellow (sometimes with red margins) and glabrous, outer surface red and glabrous to puberulous, 12–17 cm. long, 7–8 cm. wide at base, all becoming necrotic soon after anthesis, deteriorating distally first and basipetally with age. Floral bracts ± translucent at anthesis, quickly decomposing, white, puberulous to velutinous along margins abaxially, glabrous adaxially, 3.5–4.5 cm. long, 1.5–2 cm. wide at base. Flowers 8 to 13 per cincinnus; pedicel pale yellow, tomentose, 1.4–2.2 cm. long; perianth yellow to deep yellow, glabrous, puberulous along margins, 4.5–5 cm. long, 6–9 mm. wide at base, at anthesis curved 50–80°; free sepal lowermost, reflexed, fused sepals with apices slightly reflexed; staminode white, apex dentate, 1.5–2 cm. long, 4–5 mm. wide; stamens with anthers connivent partially inside apex of corolla tube; ovary pale yellow, glabrous, 5–6 mm. long, 6–7 mm. wide. Drupes blue, glabrous.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m., *Kress & Cooper-Smith 76-652* (DUKE); El Valle de Antón, behind Cerro Gaital, elev. 2200 ft., *Kress et al. 80-1158* (DUKE); mountains above El Valle, in forest on Sr. Furlon's finca, *Stimson 5037* (SCZ), *Stimson 5038* (SCZ).

PHENOLOGY. Flowering early in the rainy season (April) and probably continuing through late August.

HABITAT AND DISTRIBUTION. This species is found on steep, forested slopes at elevations of 650–1000 meters in the region of El Valle de Antón in Panama. As more collections are made in the provinces of Coclé and Veraguas, especially on the Atlantic slopes, it is expected that the known distribution will be extended.

RELATIONSHIPS. *Heliconia necrobracteata,* together with *H. trichocarpa* Daniels & Stiles, *H. colgantea* R. R. Smith ex Daniels & Stiles, and *H. maculata* Kress, is included in one of the several groups of species with small pendent inflorescences. It is distinguished by its necrotic cincinnal bracts, its glabrous ovaries, and its generally stouter vegetative shoots and inflorescences.

NAME. This species is named for its distinctive red cincinnal bracts that decompose and turn black beginning distally and progressing basipetally even while flowers are still being produced.

Heliconia sessilis Kress, sp. nov. FIGURE 4.

Planta herbacea 6–7 m. alta; inflorescentia nutans vel pendens, sessilis, rubra; pedunculus occultus; rhachis rubra vel lutea, puberula; cincinnorum bracteae spirales, rubrae, glabrae; perianthium luteum, glabrum; ovarium album, glabrum.

TYPE: Panama, Colón, along the road between Gatun Lock and Fort Sherman, elev. ca. 3 meters, 28 August 1980, *Kress 80-1241* (DUKE, holotype; F, GH, K, MO, PMA, isotypes).

Herb with *Musa*-like habit, 6 to 7 meters tall. Leafy shoots in groups of 10 to 20; pseudostem green to brown, glabrous, 2.5 meters tall, 8–9 cm. in diameter; leaves 4 or 5 per shoot; petiole olive green, glabrous, 1.4–1.8 meters long, 2 cm. in diameter; blade with base unequal and attenuate to obtuse, apex acute, the upper surface green, glabrous, with midrib olive green and glabrous, the lower surface dull green, glaucous, with midrib yellow-green with central maroon stripe and slightly glaucous, the longest blade 2 meters long, 40–60 cm. wide. Inflorescence nodding to pendent, to 90 cm. long; peduncle obscure, red, puberulous, 2 cm. in diameter; rachis flexuose, red at base of inflorescence becoming yellow toward distal bracts, puberulous, 1.8–1.9 cm. in diameter at base; cincinnal bracts spirally arranged, 23 to 30 per inflorescence, oriented 90° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acute, margins straight becoming involute near rachis, inner surface white to pink and glabrous to puberulous, outer surface red and glabrous, 8–9 cm. long, 9 cm. wide at base. Floral bracts opaque, persistent, pale yellow becoming pink along margins, puberulous abaxially, glabrous adaxially, 3.5–4 cm. long, 1.8–2.1 cm. wide at base. Flowers 15 to 20 per cincinnus; pedicel white becoming reddish near ovary, glabrous, 6–10 mm. long; perianth distally deep yellow becoming paler at base, glabrous except for puberulous sepal margins, 4.8–5.1 cm. long, 1.1–1.2 cm. wide at base, at anthesis curved 30–40°; free sepal lowermost, reflexed, fused sepals with apices reflexed; staminode white to pale yellow, apex cuspidate, 6–7 mm. long, 3 mm. wide; stamens with anthers connivent inside apex of corolla tube; ovary white becoming pale lavender around apex, glabrous, 1–1.2 cm. long, 6–7 mm. wide. No mature fruits seen.

SPECIMENS EXAMINED. **Panama.** CANAL ZONE: vic. of Fort Sherman, W. of Colón, near sea level, *Kress & Clarkson 77-871* (DUKE); Barro Colorado Is., laboratory clearing, *Croat 12422* (MO, NY, SCZ).

PHENOLOGY. Flowering during the wettest part of the rainy season in Panama, from late August probably to December.

HABITAT AND DISTRIBUTION. This species is found in flooded secondary growth in the Atlantic coastal lowlands of Panama. Only a very localized population has been found west of Colón, but this species may be scattered farther east in Panama and even into South America.

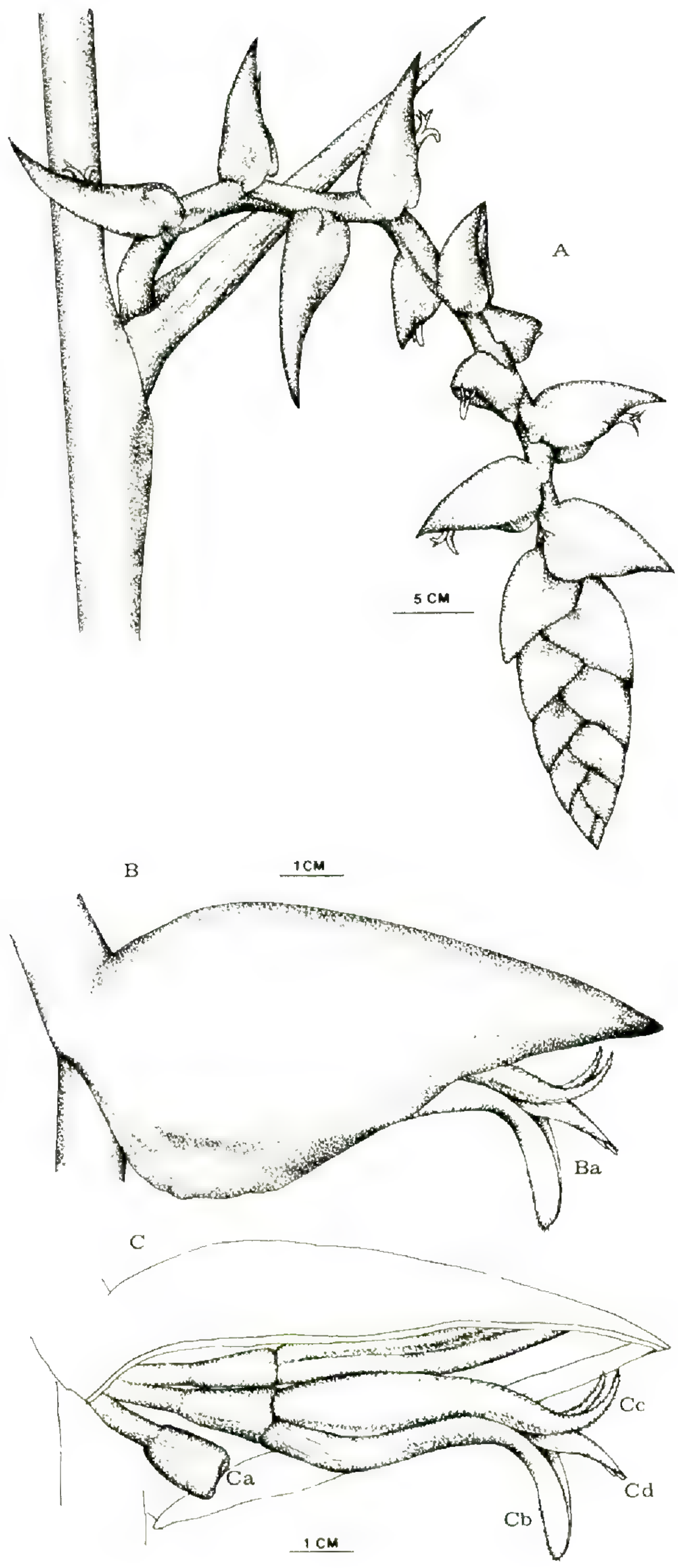

FIGURE 4. **Heliconia sessilis.** A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing two sepals fused to partially spread-open corolla tube. G, H, staminodes: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

RELATIONSHIPS. *Heliconia sessilis* fits into the group with large shoots and pendent inflorescences, including *H. pogonantha* Cufod. and *H. longa* (Griggs) Winkler, but probably has its closest relatives in South America. It is characterized by its sessile inflorescence, by its only slightly curved (30–40°) perianth, and by its occurrence in semi-aquatic habitats.

NAME. This species is named for the distinctive sessile nature (reduced peduncle length) of the inflorescence, which causes the basal cincinnal bracts to open upward and the more distal bracts to open downward.

Heliconia xanthovillosa Kress, sp. nov. FIGURE 5.

Planta herbacea 3.5–4.5 m. alta; inflorescentia pendens, lutea vel viridi-lutea, pubescentia lanata flava praedita; cincinnorum bracteae distichae; perianthium basi album, apice lutescens pubescentia lutea praedita; ovarium album, glabrum; fructus caeruleus, glabrus.

TYPE: Panama, Panamá, El Llano–Carti Road, 12 km. from intersection with Pan American Hwy., elev. 500 meters, 27 August 1980, *Kress & Knapp 80-1233* (DUKE, holotype; F, GH, K, MO, PMA, isotypes).

Herb with *Musa*-like habit, 3.5–4.5 meters tall. Leafy shoots in groups of 2 to 11; pseudostem brown, scurfy to hirsute, 1.6–1.9 meters tall, 6–6.5 cm. in diameter; leaves 4 per shoot; petiole dull green, glabrous, 1.1–1.2 meters long, 1.9–2 cm. in diameter; blade with base unequal and obtuse to truncate, apex acute, the upper surface green to dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.3 meters long, 49–52 cm. wide. Inflorescence pendent, to 86 cm. long (excluding peduncle); peduncle bright yellow-green, woolly with yellow hairs, 26–68 cm. long, 1.5–2.2 cm. in diameter; rachis flexuose, bright yellow, woolly, 1.5–1.9 cm. in diameter at base; cincinnal bracts distichous, up to 35 per inflorescence, oriented 35–45° to axis of inflorescence, the basal bract sterile or fertile, the middle bract with apex acuminate to acute, margins straight, inner surface pale yellow-green and pubescent, outer surface bright yellow to green-yellow and woolly with yellow hairs, 8–10 cm. long, 7–8 cm. wide at base. Floral bracts opaque, persistent through fruiting, pale yellow, pubescent abaxially, glabrous adaxially, 3.7–4.8 cm. long, 1.6–1.7 cm. wide at base. Flowers 12 to 20 per cincinnus; pedicel white, glabrous, 1 cm. long; perianth white basally becoming yellow distally, glabrous basally becoming pubescent with bright yellow hairs distally, 5.1–5.5 cm. long, 9–11 mm. wide at base, at anthesis curved 85–90°; free sepal lowermost, reflexed, fused sepals with apices slightly reflexed; staminode white, apex acuminate, 5 mm. long, 3 mm. wide; stamens with anthers connivent inside apex of corolla tube; ovary white, glabrous, 7–8 mm. long, 5–6 mm. wide. Drupes blue, glabrous, 1.1–1.2 cm. long, 8 mm. wide; stones 8–9 mm. long, 5–6 mm. wide.

SPECIMENS EXAMINED. **Panama.** PANAMÁ. El Llano–Carti Rd.: 8 mi. from Pan American Hwy., elev. 1200 ft., *Antonio 1699* (MO), elev. 300–500 m., *Folsom*

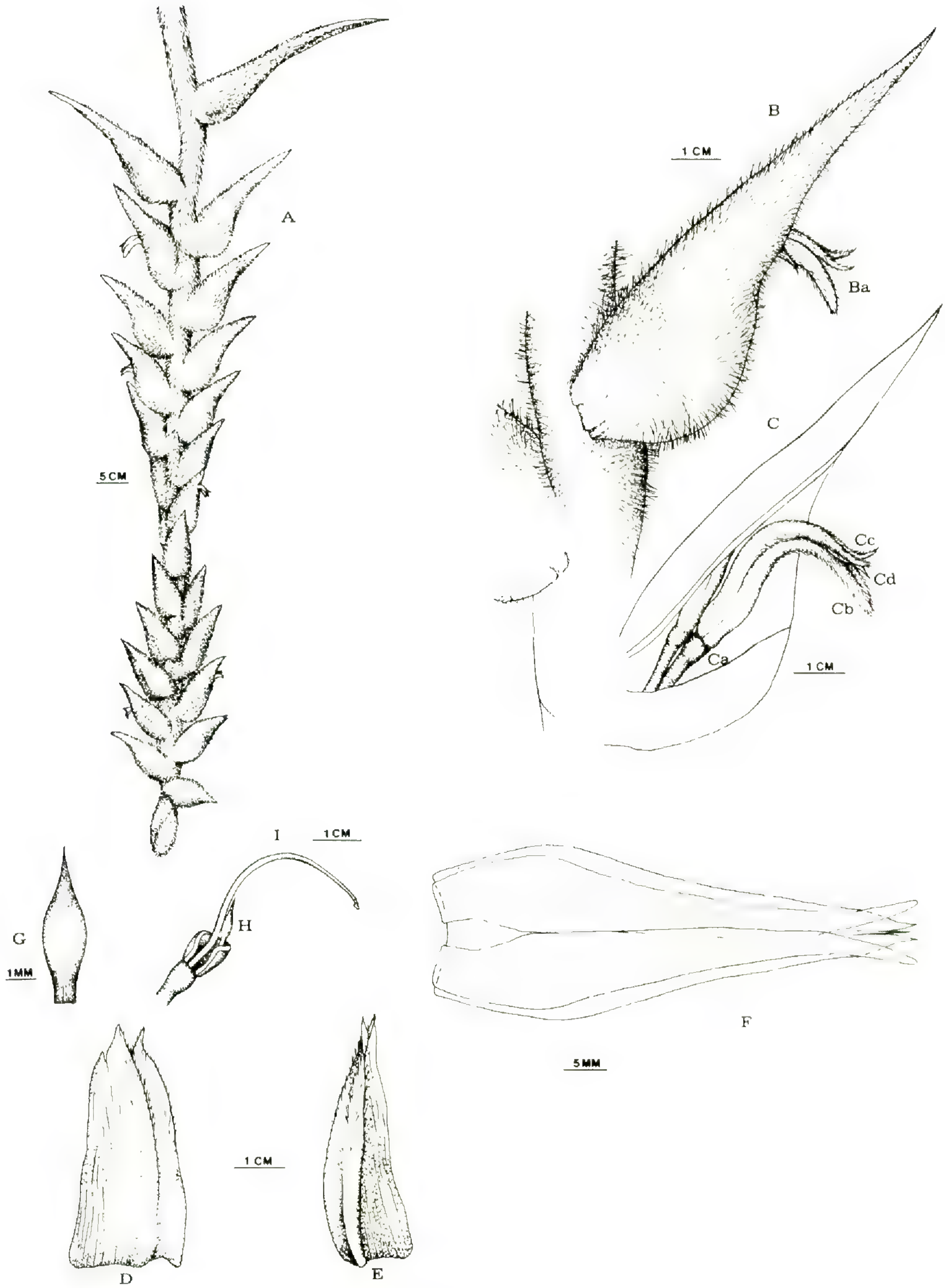

FIGURE 5. **Heliconia xanthovillosa.** A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing two sepals fused to partially spread-open corolla tube. G, H, staminodes: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

& Maas 5214 (MO), without further location, *Antonio 1266* (MO), *Folsom 3507* (MO).

PHENOLOGY. Flowering during the rainy season in Panama from late May to October; most likely producing fruit well into November.

HABITAT AND DISTRIBUTION. This species is found at middle elevations (ca. 500 m.) in open areas in the forest, and now especially in areas disturbed by man. It has been collected only along the continental divide separating the drier Pacific slopes from the wetter Atlantic slopes of Eastern Panama above the Río Carti.

RELATIONSHIPS. *Heliconia xanthovillosa* is closely related to species of the pogonantha group, including *H. vellerigera* Poeppig, *H. ramonensis* Daniels & Stiles, and *H. magnifica* Kress, which differ from each other essentially in bract and indumentum color and in bract orientation. *Heliconia xanthovillosa* has bright greenish yellow inflorescences with long, yellow hairs covering the peduncle, rachis, and distichous cincinnal bracts.

NAME. This species is named for the beautiful yellow hairs that are conspicuous on the entire inflorescence in both living and dried material.

Heliconia collinsiana Griggs var. **velutina** Kress, var. nov.

A var. collinsiana in planta 6 m. alta, folio pagina inferiore glabra, pedunculo et rhachidi villosa, et perianthio aurantiaco, differt.

TYPE: Guatemala, Quezaltenango, lower slopes of Volcán Santa María de Jesús, along highway to Quezaltenango near Santa María de Jesús, elev. 1450 meters, 30 June 1977, *Kress, Clarkson, & McDade 77-756* (DUKE, holotype; F, K, isotypes).

Herb with *Musa*-like habit, to 6 meters tall. Leafy shoots in groups of 3 to 8; pseudostem glabrous to tomentose, 2.5–3 meters tall, 7 cm. in diameter; leaves 3 or 4 per shoot; petiole green, glaucous, 1–1.2 meters long, 2.5–3 cm. in diameter; blade with base unequal and obtuse, apex acute, the upper surface dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous, with midrib light green with central maroon stripe and glaucous, the longest blade 2.2–2.5 meters long, 65–70 cm. wide. Inflorescence pendent, to 70 cm. long (excluding peduncle); peduncle rusty red, villous to velutinous with rusty hairs, 16–30 cm. long, 1.5–1.9 cm. in diameter; rachis flexuose, red, tomentose to velutinous, 1.1–1.3 cm. in diameter at base; cincinnal bracts spirally arranged, 15 to 18 per inflorescence, oriented 80–90° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acuminate, margins revolute, inner surface red and glabrous, outer surface deep red and glabrous, 14–17 cm. long, 6–7.5 cm. wide at base. Floral bracts opaque and quickly decomposing after anthesis, white, glabrous to puberulous abaxially, glabrous adaxially, 5–6 cm. long, 1.5–2.5 cm. wide at base. Flowers 15 to 20 per cincinnus; pedicel pale orange, puberulous, 1–1.7 cm. long; perianth pale orange becoming reddish along

sepal margins, glabrous to puberulous, 5.5–5.7 cm. long, 8–9 mm. wide at base, at anthesis curved 15–20°; free sepal lowermost, reflexed, fused sepals with apices not reflexed; staminode white, apex tridentate with central tooth longer than lateral ones, 9–12 mm. long, 4–5 mm. wide; stamens with anthers flared outside perianth apex; ovary pale green, glabrous, 7–8 mm. long, 7–9 mm. wide. Drupes metallic blue, glabrous, 1.2–1.5 cm. long, 1.6–1.8 cm. wide.

SPECIMENS EXAMINED. **Guatemala.** ESCUINTLA: Finca Monterrey, S. slope of Volcán de Fuego, elev. 1140–1260 m., *Standley 64533* (F). QUEZALTENANGO: road to Finca Pireneos near Santa María de Jesús, elev. 4000 ft., *Kress et al. 76-663* (DUKE); Volcán Santa María, elev. 4500 ft., *Kellerman 6073* (F); Volcán Santa María de Jesús, elev. 4500 ft., *Kellerman 6076* (US); Finca Pireneos below Santa María de Jesús, elev. 1350–1380 m., *Standley 68427* (F); between Finca Pireneos and Finca Soledad, lower south-facing slopes of Volcán Santa María between Santa María de Jesús and Calahuache, elev. 1300–1400 m., *Steyermark 33575* (F). SANTA ROSA: Cenaguilla, elev. 4000 ft., *Heyde & Lux 4635* (GH, US). SUCHITEPEQUEZ: Finca Mocá, in bushy growth at edge of barranca, elev. 5000 ft., *Skutch 2101* (GH). **El Salvador.** AHUACHAPÁN: Sierra de Apaneca in region of Finca Colima, *Standley 20081* (US). SANTA ANA: moist canyon slope, W. side of Cerro del Aguila, elev. 1650 m., *Tucker 1291* (F, UC, US). SONSONATE: Cerro los Naranjos, *ITICSS 1207* (MO).

PHENOLOGY. Flowering and fruiting mainly during the dry season (January to April) and the early part of the rainy period (May to July), but with some inflorescences usually produced at any time of the year.

HABITAT AND DISTRIBUTION. *Heliconia collinsiana* var. *velutina* is found on steep, forested slopes at middle to higher elevations (above 1300 m.) in the Guatemalan and Salvadorian highlands. It is one of the few species of *Heliconia* found at such high elevations.

RELATIONSHIPS. This variety is distinguished from var. *collinsiana* by its overall greater stature, lack of glaucous lower leaf surfaces, hairy peduncle and rachis, orange flowers, and distribution at higher elevations.

NAME. "Velutina" was used as a varietal epithet by both I. Lane and R. R. Smith but was never validly published by either. Here it is used since it is descriptive of the velutinous nature of the peduncle and rachis.

Heliconia pogonantha Cufod. var. **veraguasensis** Kress, var. nov.

A var. pogonantha in planta 4–4.5 m. alta, folia pagina inferiore purpurascenti et inflorescentia glabra vel villosa, differt.

TYPE: Panama, Veraguas, 2 miles above Santa Fé beyond the Agricultural School, elev. 850 meters, 9 August 1977, *Kress, Clarkson, & McDade 77-825* (DUKE, holotype; K, MO, isotypes).

Herb with *Musa*-like habit, 4–4.5 meters tall. Leafy shoots in groups of 3 to 15; pseudostem scurfy, 1.3–1.7 meters tall, 5 cm. in diameter; leaves 3 or 4 per shoot; petiole yellow-green, glabrous, 1–1.2 meters long, 1.5–1.8

cm. in diameter; blade with base unequal and truncate to cordate, apex acute, the upper surface dark green, glabrous, with midrib yellow-green and glabrous, the lower surface green, tinged with maroon especially along margins, glabrous, with midrib yellow-green and glabrous to scurfy, the longest blade 1.2–1.5 meters long, 40–45 cm. wide. Inflorescence pendent, to 75 cm. long (excluding peduncle); peduncle yellow, scurfy to villous, 10–30 cm. long, 1.8–2 cm. in diameter; rachis flexuose, yellow, puberulous to villous, 1.8–1.9 cm. in diameter at base; cincinnal bracts spirally arranged, 20 to 25 per inflorescence, oriented 45–65° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acuminate, margins straight, inner surface reddish yellow and tomentose, outer surface red becoming yellow near rachis and glabrous to puberulous, 9–10.5 cm. long, 8–9 cm. wide at base. Floral bracts opaque, persistent, pale yellow, tomentose to velutinous with golden hairs abaxially, glabrous adaxially, 4–4.8 cm. long, 1.5–2.5 cm. wide at base. Flowers 10 to 15 per cincinnus; pedicel white to yellow, puberulous, 7–12 mm. long; perianth yellow, glabrous basally becoming densely velutinous with golden hairs distally especially along sepal margins, 5.4–5.7 cm. long, 1–1.1 cm. wide at base, at anthesis curved 80–90°; free sepal lowermost, fused sepals with apices reflexed; staminode white, apex acuminate, 6–7 mm. long, 3 mm. wide; stamens with anthers connivent inside apex of corolla tube, ovary white to pale yellow, glabrous, 8–9 mm. long, 5–6 mm. wide. Mature fruits not seen.

SPECIMENS EXAMINED. **Panama.** VERAGUAS: vic. of Santa Fé, forested slopes of Cerro Tute, elev. 3000 ft., *Allen 4333* (MO); road between Santa Fé and Río Calovebora, 1.8 mi. beyond Escuela Agricola Alto Piedra, elev. 735 m., *Croat & Folsom 34255* (MO); shoulder of Cerro Tute, *Folsom & Edwards 3355* (MO); beyond Escuela Agricola above Santa Fé, elev. 2600 ft., *Kress & Cooper-Smith 76-655* (DUKE), *Kress & Cooper-Smith 76-656* (DUKE), elev. 2800–4600 ft., *Kress et al. 80-1189* (DUKE); beyond Santa Fé along road to Calovebora, Pacific slopes, elev. 2200 ft., *Kress et al. 80-1200* (DUKE); lower montane wet forest 7 km. W. of Santa Fé, elev. 2900 ft., *Nee 11207* (US).

PHENOLOGY. Flowering from March to September, but at least a few individuals are flowering and fruiting at most times of the year.

HABITAT AND DISTRIBUTION. *Heliconia pogonantha* var. *veraguasensis* is restricted to middle elevation (735–1000 m.) wet forests and secondary growth in the vicinity of Cerro Tute on the Pacific slopes in Veraguas, Panama.

RELATIONSHIPS. *Heliconia pogonantha* is widespread in Central and South America, with many geographic varieties throughout its range. Var. *veraguasensis* is distinctive in its inflorescence with variable vestiture, its lower leaf surfaces tinged with maroon, and its overall stature smaller than that of the other varieties.

NAME. This taxon was given specific status by both I. Lane and R. R. Smith under the name of *Heliconia paulii,* but that combination was never validly published. Here it is designated as a variety and given the name "veraguasensis" after the province in Panama where it occurs.

Heliconia ramonensis Daniels & Stiles var. **xanthotricha** Kress, var. nov.

A var. ramonensi in pubescentia lutea, pedunculo rubro-aurantiaco, et cincinnorum bracteis roseis, differt.

TYPE: Panama, Coclé, 6 miles beyond El Valle de Antón behind Cerro Gaital, elev. 900 meters, 13 August 1977, *Kress, Clarkson, & McDade 77-840* (DUKE, holotype; K, MO, isotypes).

Herb with *Musa*-like habit, 4–5 meters tall. Leafy shoots in groups of 3 to 10; pseudostem orange to brown, glabrous to villous, 1.3–2 meters tall, 5–8 cm. in diameter; leaves 3 to 5 per shoot; petiole green, glabrous, 1–1.2 meters long, 1.5–2 cm. in diameter; blade with base unequal and truncate to cordate, apex acute, the upper surface dark green, glabrous, with midrib yellow-green and glabrous, the lower surface green, tinged with maroon especially along margins, glabrous, with midrib yellow-green and glabrous, the longest blade 1.3–1.8 meters long, 40–60 cm. wide. Inflorescence pendent, to 90 cm. long (excluding peduncle); peduncle red, woolly with golden-yellow hairs, 30–50 cm. long, 1.6–2 cm. in diameter; rachis semiflexuose, red-orange, villous to velutinous with yellow hairs, 1.5–2.2 cm. in diameter at base; cincinnal bracts distichous or spirally arranged, 20 to 40 per inflorescence, oriented 40–45° to axis of inflorescence, the basal bract sometimes sterile, the middle bract with apex acute, margins straight becoming involute at base, inner surface pink and velutinous to villous, outer surface rose-red and glabrous to villous, 9–12 cm. long, 7–10 cm. wide at base. Floral bracts opaque, persistent, white to pink, villous to velutinous with bright yellow hairs abaxially, glabrous adaxially, 4–5 cm. long, 1.5–3 cm. wide at base. Flowers 10 to 15 per cincinnus; pedicel white to pink, glabrous, 7–13 mm. long; perianth white basally becoming yellow distally, glabrous basally becoming tomentose to velutinous with bright yellow hairs distally, especially along sepal margins, 5–6 cm. long, 1–1.2 cm. wide at base, at anthesis curved 90°; free sepal lowermost, fused sepals with apices reflexed; staminode white, apex caudate to acuminate, 7–8 mm. long, 2–3 mm. wide; stamens with anthers connivent inside apex of corolla tube; ovary bluish white, glabrous, 8–10 mm. long, 5–6 mm. wide. Drupes dark blue, glabrous, 1.3–1.5 cm. long, 9–10 mm. wide.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m., *Kress & Cooper-Smith 76-651* (DUKE); hills near El Valle de Antón, elev. 800 m., *Maas et al. 1725* (MO, US); vic. of El Valle, elev. 800–1000 m., *Allen 1818* (MO); mountains N. of El Valle de Antón, elev. 2500–3000 ft., *Lewis et al. 1750* (MO); 8 mi. N. of El Valle de Antón, *Luteyn & Kennedy 1718* (DUKE, MO); region of El Valle de Antón on trail to Las Minas, elev. 1000 m., *Allen 2867* (US); Las Minas, *Allen 2707* (MO); El Valle de Antón, vic. Finca Tomas Arias, elev. 600 m., *Allen 3629* (US); foot of Cerro Pilón, above El Valle de Antón, elev. 2000 ft., *Porter et al. 4423* (SCZ, UC); below Cerro Pilón, *Croat 13471* (MO); La Mesa, 2.8–3.4 mi. NW. of El Valle de Antón, elev. 850–900 m., *Luteyn 4064* (DUKE); La Mesa, elev. 810 m., *Croat 25311* (MO), elev. 900 m., *Croat 22952* (MO), without further location, *Croat 14374* (MO, SCZ); La Mesa, near El Valle, *Antonio*

1292 (MO); La Mesa, 2 km. W. of Cerro Pilón, elev. 900 m., *Sullivan 541* (MO); ca. 9 km. from El Valle market beyond Sr. Furlong's Finca, *Kennedy et al. 3223* (DUKE, MO); Cerro Gaital, N. of El Valle, elev. 760 m., *Reveal & Balogh 4971* (MO); El Valle de Antón, behind Cerro Gaital, elev. 2200 ft., *Kress et al. 80-1161* (DUKE); N. rim of El Valle de Antón, near Cerro Turega, elev. 650–700 m., *Woodson & Schery 205* (MO); area surrounding Rivera sawmill, 7 km. N. of El Cope, continental divide, elev. 750–850 m., *Folsom & Collins 6430* (MO); forests along Río Boqueron above Peluca Hydrographic Station, elev. ca. 90 m., *Hunter & Allen 659* (MO).

PHENOLOGY. Flowering mainly during the rainy season from May to September, but some inflorescences are produced throughout the year.

HABITAT AND DISTRIBUTION. *Heliconia ramonensis* var. *xanthotricha* is found at middle elevations (650–1000 meters) on moist, forested slopes and often invades more disturbed open areas. Its distribution is localized in Coclé, Panama, in the region around El Valle de Antón.

RELATIONSHIPS. *Heliconia ramonensis* var. *xanthotricha* differs from var. *ramonensis* of Costa Rica in its distinctively yellower vestiture, especially on the peduncle, rachis, and floral bracts, and in the contrasting colors of the orange-red rachis and the rose-red cincinnal bracts.

NAME. Both I. Lane and R. R. Smith recognized this taxon as specifically distinct from other heliconias and referred to it as *Heliconia xanthotricha* because of the bright yellow hairs on various parts of the inflorescence. However, neither investigator published the name. Daniels and Stiles named a very similar taxon from Costa Rica as *H. ramonensis*. Therefore, I have used the descriptive epithet employed invalidly by both Lane and Smith and have published it as *H. ramonensis* var. *xanthotricha*.

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I would like to thank Drs. D. E. Stone and R. L. Wilbur for help with the descriptions; Dr. W. L. Culberson for sharing his expertise in botanical Latin; Drs. F. G. Stiles and G. S. Daniels for informative taxonomic discussions; Sally Anderson for her critical eye in preparing the line drawings; T. Antonio and J. Abalo, who first showed me photographs of *Heliconia xanthovillosa;* and Dr. L. L. Clarkson for her companionship in the field. Curators of the following herbaria have kindly made collections available: CR, DUKE, F, GH, MO, NY, PMA, SCZ, UC, and US. The research was supported by National Science Foundation grants DEB77-01556 to W. J. Kress and D. E. Stone and DEB77-24612 to D. E. Stone, and by Biomedical Research Support Grant No. 303-3806 to D. E. Stone.

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A NEW SPECIES OF ATELEIA (LEGUMINOSAE) FROM THE BAHAMAS

DONOVAN S. CORRELL

IN RECENT YEARS the Bahama flora has been the subject of intensive investigation. One of the results of careful field study has been the discovery or elucidation of several localities where rare or unusual species occur. These localities are believed to represent refugia where survival has been possible for these plants despite what may be—or may previously have been—an otherwise unfavorable environment. *Wallenia laurifolia* Sw. on Grand Bahama, *Tabernaemontana citrifolia* L. on Eleuthera, *Celtis iguanaea* (Jacq.) Sarg. on South Andros, and *Ctenitis hirta* (Sw.) Copel. on New Providence are examples of such presumed refugia species. The plant now being described not only survives in such a refuge area, but also apparently is a species previously unknown in *Ateleia* (Moç. & Sessé ex DC.) D. Dietr., a very distinct and natural genus.

Dr. Robert H. Mohlenbrock, who monographed *Ateleia* in 1962, was sent material of this plant but declined to advance an opinion regarding its identity. It is more closely related to such species as the Cuban *Ateleia apetala* Griseb. than to the only other species of this genus known from the Bahamas, *A. gummifera* (DC.) A. Dietr.

Ateleia popenoei Correll, sp. nov. FIGURE 1.

Arbor ad 5 m. alta, corona lata ramorum gracilium. Truncus erectus glaber, cortice cineraceo ad fumeo; rami et ramuli cineracei, pilis brevibus adpressis porrectis et lenticellis conspicuis. Foliola 5 ad 11, tenui-herbacea, alterna vel subopposita; petioluli graciles, 3–4 mm. longi, circa 0.5 mm. crassi, puberuli; laminae typice orbiculo-ovatae ad elliptico-lanceolatae, ad circa 6 cm. longae et 2.5 cm. latae, plerumque multo breviores, vulgo oblique ad basem rotundatae et ad apicem obtusae ad acutae, integrae, prasinae, nervo medio prominente, venatione minute reticulata. Flores et fructus generis typici.

TYPE: Bahamas, Great Exuma, on a high, coppice-covered rocky ridge above roadway west of Moss Town, saplings and trees to 5 m. tall, October 3, 1980. *D. S. Correll & John Popenoe 51420* (A, holotype; F, FTG, NY, US, isotypes).

Tree to 5 meters tall, with widespreading crown of slender branches. Trunk erect, smooth, with light gray to grayish brown bark; branches and branchlets grayish, with short, appressed, porrect hairs and conspicuous lenticels. Leaves exstipulate, alternate or subopposite; petioles slender, to about 3 cm. long;

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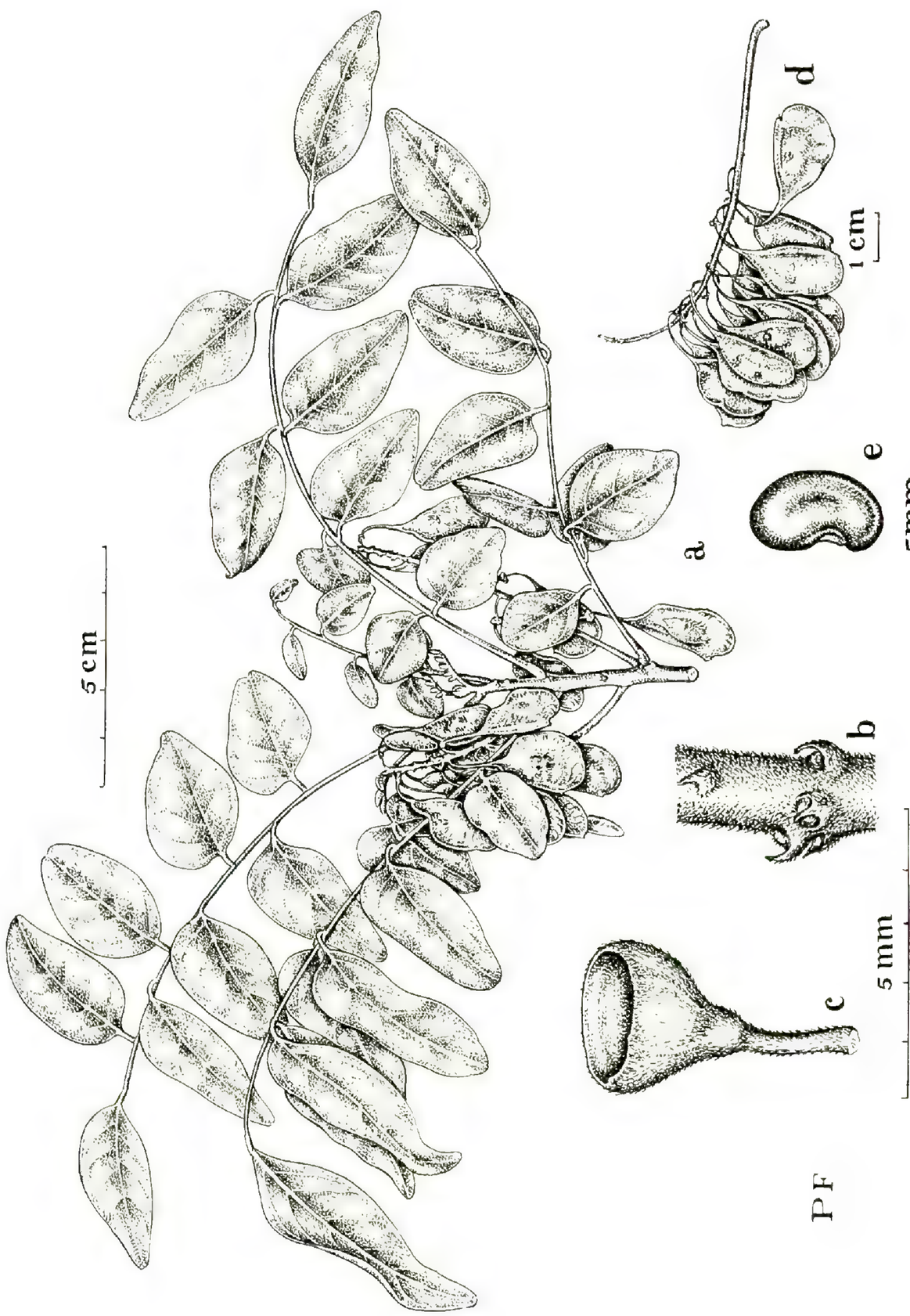

FIGURE 1. **Ateleia popenoei:** a, fruiting branchlet; b, section of fruiting rachis; c, pedicel and calyx; d, fruiting inflorescence; e, seed. (Solitary petals, stamens, and pistils too disfigured by insects to be drawn.) *Drawn by Priscilla Fawcett.*

blades odd-pinnate, oblong-elliptic, to about 20 cm. long; rachis slender, terete, with short, appressed, porrect hairs. Leaflets 5 to 11, thin-herbaceous, alternate or subopposite; petiolules slender, 3–4 mm. long, about 0.5 mm. thick, puberulent; blades typically orbicular-ovate to elliptic-lanceolate, to about 6 cm. long and 2.5 cm. wide, mostly much smaller, usually obliquely rounded at base and obtuse to acute at apex, entire, bright green, with prominent central vein and faint, minute reticulations. Flowers cream, in rather dense axillary racemes to about 10 cm. long; floral bracts triangular-subulate, acute, incurved, mostly less than 1 mm. long; pedicels slender, to about 3 mm. long. Calyx cup shaped, about 2 mm. high, with an even, truncate apex. Petal 1; claw about 3 mm. long; blade about 3 mm. long, cucullate, about 4 mm. wide when spread out. Stamens 10, free; filaments 3 mm. long; anthers ovate to elliptic, about 1.3 mm. long. Fruit with slender, glabrous stipe 6–8 mm. long that is expanded into the 1-seeded, obliquely semiorbicular to semicordate legume; legume glabrous, flattened, reticulate veined, about 2 cm. long and 1.3 cm. wide, narrow wing along upper suture about 1.5 mm. wide and extending to within 2–3 mm. of apex. Seed reniform-elliptic, turgid, 4–5 mm. long, dark reddish brown.

The small, thin-herbaceous leaflets with slender, elongate petiolules and typically ovate to ovate-elliptic, weakly reticulate-veined, basally broadly rounded blades are most characteristic. Those species of *Ateleia* most closely allied to *A. popenoei,* especially *A. apetala* of Cuba, have rather large, subcoriaceous to thick-membranaceous leaflets with thick, shortened petiolules, and typically elliptic-lanceolate, strongly reticulate-veined blades that are cuneate or very narrowly rounded at base.

It is a pleasure to name this species for Dr. John Popenoe, Director of the Fairchild Tropical Garden, whose broad knowledge of the flora of the Bahama Islands enabled him to recognize the uniqueness of this plant.

ACKNOWLEDGMENTS

I am indebted to the National Science Foundation for a grant (No. DEB-7402135) in support of my work on the flora of the Bahamas, Turks and Caicos Islands. The excellent drawing is that of Priscilla Fawcett, Staff Artist of the Fairchild Tropical Garden, to whom I am most grateful. I also wish to thank my wife and colleague, Dr. Helen B. Correll, for her contributions to my research.

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CALYCANTHUS FLORIDUS (CALYCANTHACEAE)—A NOMENCLATURAL NOTE

D. E. Boufford and S. A. Spongberg

In his revisionary study of the Calycanthaceae, Nicely (1965) recognized a single eastern North American species of *Calycanthus,* which comprises two varieties, *C. floridus* L. var. *floridus* and *C. floridus* var. *laevigatus* (Willd.) Torrey & Gray. This treatment has been either adopted independently or followed by Radford, Ahles, and Bell (1964, 1965, 1968) and Strausbaugh and Core (1978), and subsequently by most, if not all, collectors in the southeastern United States. Although Nicely's treatment may oversimplify the variation patterns present in *Calycanthus* in the eastern United States (cf. Wood, 1958), we are not prepared at this time to refute his taxonomic scheme. However, we should like to draw attention to the fact that *laevigatus* is not the earliest varietal epithet available[1] when Nicely's treatment of *C. floridus* is followed.

Torrey and Gray (1840) were the first to use *laevigatus* as a varietal epithet under *Calycanthus floridus* when they reduced *C. laevigatus* Willd., *C. glaucus* Willd., and *C. inodorus* Ell. to varietal standing. Since Nicely's circumscription of plants of *C. floridus* with glabrous lower leaf surfaces includes both glaucous and nonglaucous forms, it appears that his choice of *laevigatus* (rather than *glaucus* or *inodorus*) as the varietal epithet was based on a desire to use an all-inclusive, descriptive epithet.

Nuttall (1818), however, recognized four taxa of *Calycanthus* in eastern North America—three species (*C. floridus, C. glaucus,* and *C. laevigatus*) and one variety (*C. glaucus* var. *oblongifolius* Nutt.). Since Nicely considered *C. glaucus* var. *glaucus, C. glaucus* var. *oblongifolius, C. floridus* var. *glaucus,* and *C. floridus* var. *laevigatus* (as well as *C. floridus* var. *inodorus*) to be synonyms that apply to the same taxon, Nuttall's epithet *oblongifolius* must be considered when determining the correct name of the variety of *C. floridus. Oblongifolius* (1818) predates Torrey and Gray's usage of *glaucus, inodorus,* and *laevigatus* (all 1840) as varietal epithets by 22 years and therefore has priority as the earliest available varietal epithet for plants of *C. floridus* with glabrous leaf undersurfaces as circumscribed by Nicely. For this reason the following new combination is necessitated.

Calycanthus floridus L. var. **oblongifolius** (Nutt.) D. E. Boufford & S. A. Spongberg, comb. nov.

[1] Article 60 of the International Code of Botanical Nomenclature (Regnum Vegetabile **97:** 51. 1978) states that "when the rank of a genus or infrageneric taxon is changed, the correct name or epithet is the earliest legitimate one available in the new rank. In no case does a name or epithet have priority outside its own rank."

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BASIONYM: *Calycanthus glaucus* Willd. var. *oblongifolius* Nutt. Gen. N. Am. Pl. **1:** 312. 1818.

Synonyms, which should include *Calycanthus floridus* var. *laevigatus,* can be found in Nicely (1965).

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NOTICE

Because of continually increasing production costs, the Editorial Committee of the *Journal of the Arnold Arboretum* is requesting authors to help defray publication expenses. Beginning with manuscripts received and accepted for publication as of March, 1980, a page charge will be levied. Acceptance of manuscripts for the Journal will, however, continue to be based solely on appropriateness and scientific merit, not on an author's ability to meet page costs. Information on page charges and general editorial policies can be obtained from the Managing Editor.

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THE GENERA OF AMARANTHACEAE IN THE SOUTHEASTERN UNITED STATES[1]

KENNETH R. ROBERTSON

AMARANTHACEAE A. L. Jussieu, Gen. Pl. 87. 1789, "Amaranthi," nom. cons.

(AMARANTH FAMILY)

Annual or perennial herbs, often woody at the base, infrequently lianas [or shrubs or trees]; stems erect to decumbent, trailing, or climbing, simple or much branched, unarmed or rarely spinescent, glabrous to densely pubescent, [very rarely fleshy and/or articulated], usually from a stout taproot. Leaves alternate or opposite, simple and usually entire, sometimes undulate, infrequently serrulate or shallowly lobed, [very rarely reduced to scales or absent], long-petiolate to sessile; stipules absent. Inflorescences of compact cymes or clusters arranged in axillary or terminal, simple or compound spikes, panicles, heads, or rarely racemes, or the flowers solitary; foliage leaves often reduced and bractlike in the inflorescence; each flower subtended by 1 bract and usually 2 bracteoles, all usually scarious, often spinescent, the

[1]Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum of Harvard University. This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

This paper was initiated while I was at the Arnold Arboretum, but it has been written largely with the generous support of the Illinois Natural History Survey. In addition to the libraries of the Arnold Arboretum and the Gray Herbarium, the library of the University of Illinois has been invaluable for checking the voluminous references. The libraries and herbaria of the Field Museum of Natural History and of the Missouri Botanical Garden were also utilized in this study, and specimens of *Amaranthus* were

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bract persistent and the bracteoles either falling with the fruit or persistent. Flowers quite small, regular, perfect or imperfect (the plants then monoecious, dioecious, or polygamous), sometimes aborted [or reduced to hooked spines]. Tepals usually 4 or 5, rarely absent, free or partly connate at the base, equal to somewhat unequal, imbricate in aestivation, usually dry and scarious or chartaceous, sometimes indurated, glabrous to densely pubescent, usually persistent around the fruit and falling either with or without it. Androecium of (1–)4 or 5 antetepalous, included (or rarely exserted) stamens; filaments free or (more commonly) basally connate into a cup or tube, the free portions linear to variously dilated, a nectariferous disc sometimes present at base of cup or tube; anthers dorsifixed, introrse, opening by longitudinal slits, either 4-locular with 2 lines of dehiscence or 2-locular with a single line of dehiscence; staminodia sometimes present in functionally carpellate flowers; pseudostaminodia present or absent, when present, of variously shaped, entire to laciniate lobes alternating with the filaments on the staminal tube; pollen grains pantoporate, trinucleate. Gynoecium of 2 or 3 united carpels; ovary superior, 1-locular, often somewhat compressed [rarely lobed]; style usually 1, terminal, elongate to very short or absent, infrequently indurate; stigmas entire and capitate or 2- or 3-lobed with the segments capitate to subulate and erect to divergent, persistent; ovules 1 or several, campylotropous or amphitropous, bitegmic, crassinucellate, inserted on short to elongate funiculi from a basal placenta and either suspended with the micropyle upward or erect with the micropyle downward. Fruit a dry, 1- to several-seeded, indehiscent, circumscissile, or irregularly dehiscent utricle or pyxis [rarely a berry or drupe]. Seeds small, mostly lenticular, subglobose, or subreniform, brown to black, erect or inverted, [sometimes enclosed by a small to large and bivalved aril], the testa usually shining, crustaceous; embryo peripheral, surrounding the mealy (farinaceous) perisperm; cotyledons incumbent; radicle superior or inferior. Embryo sac development of the Polygonum type. TYPE GENUS: *Amaranthus* L.

About 65 genera and 900 species, nearly cosmopolitan in distribution, but evidently absent from arctic and alpine habitats, most abundant in the tropics, subtropics, and warm-temperate regions. The number of genera is usually

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kindly lent by the University of Florida. Special thanks go to Dr. Carroll E. Wood, Jr., who reviews each paper in the Generic Flora series as thoroughly as though it were his own. The editorial expertise of Dr. Stephen A. Spongberg and of Ms. Elizabeth B. Schmidt is also appreciated. Ms. Laurie B. Feine has kindly read the treatments of *Amaranthus*, *Celosia*, and *Gomphrena* and has offered several suggestions and references. The plates of *Achyranthes* and *Iresine* were drawn by Karen Stoutsenberger, that of *Amaranthus* by LaVerne Trautz, and that of *Alternanthera* by Rachel A. Wheeler. All were made under the supervision of Dr. Wood, who also planned and prepared the dissections; all were prepared with the support of grants from the National Science Foundation. Living and alcohol-preserved material for the illustrations was supplied by George Avery, R. B. Channell, T. S. Elias, the late H. F. L. Rock, Allan Strahler, and C. E. Wood, Jr. The manuscript was typed by Betty Nelson, and Robbin C. Moran rechecked many of the references.

estimated to be about 65, but generic limits are not easily defined in some groups, and fewer than 60 or more than 70 genera could be recognized. At present, there seems to be a trend toward consolidation, and further study of some poorly known genera from Africa and South America may lead to more mergers. Numerous species occur in arid habitats; many are weeds; a number are found in harsh situations such as sandy, calcareous, saline, gypseous, or serpentine soils; some are found in undisturbed tropical forests; and a few are maritime, aquatic, or semiaquatic. The family is most diverse in Africa south of the Sahara Desert, southwestern North America, and Central and South America. Approximately 25 genera (about 100 species) are restricted to Africa; 16 of these have but one or two species, while the largest (*Hermbstaedtia* Reichenb. and *Pandiaka* (Moq.) Hooker f.) contain about 20 species each. The great majority of genera endemic to Africa belong to subtribe Achyranthinae (see below). About 13 genera (depending on the limits adopted) are essentially endemic to the Americas and the Galapagos Islands. Three of these (*Pleuropetalum* Hooker f., *Chamissoa* HBK., and *Pseudoplantago* Suesseng.) belong to the Amaranthoideae, the remaining ten to Gomphrenoideae-Gomphreneae. Seven of the American genera are monotypic or have only two species, but *Alternanthera* Forsskål, with an estimated 170 species, is the largest in the family. Two genera are largely endemic to Madagascar, two to the Hawaiian Islands, and three (including *Pitilotus* R. Br., which is perhaps the second largest in the family, with an estimated 100 species) to Australia. Only *Cyathula* Blume, *Iresine* P. Br., *Gomphrena* L., *Amaranthus* L., *Alternanthera,* and *Philoxerus* R. Br. were originally indigenous in both Eastern and Western hemispheres. Eleven genera (in the inclusive sense) and about 76 species of Amaranthaceae occur in the continental United States, and all of these genera except *Dicraurus* Hooker f. occur in the Southeast.

The Amaranthaceae were studied extensively by Moquin-Tandon (1849) for De Candolle's *Prodromus* and by Schinz (1893, 1934) for both editions of Engler & Prantl's *Die Natürlichen Pflanzenfamilien.* A number of new species and genera were described in numerous papers by Suessenguth, and the African and Madagascan genera were recently reviewed by Cavaco (1962, 1974). Revisionary papers have been published recently by Mears, Pedersen, Sohmer, and Townsend.

The Amaranthaceae are usually divided into subfamilies Amaranthoideae (anthers 4-locular at maturity with two lines of dehiscence) and Gomphrenoideae Schinz (anthers 2-locular at maturity with a single line of dehiscence). Schinz (1934) further divided the subfamilies into the following tribes and subtribes:

Amaranthoideae: CELOSIEAE
AMARANTHEAE: Amaranthinae and Achyranthinae
Gomphrenoideae: BRAYULINEEAE: Brayulineinae and Tidestromiinae
GOMPHRENEAE: Froelichiinae and Gomphreninae

Cavaco (1962) proposed a somewhat different scheme, recognizing four

subfamilies and five tribes, but no subtribes; unfortunately, the new categories he proposed are invalidly published since no Latin descriptions or diagnoses are either referred to or given. Cavaco's scheme, however, should be examined carefully by future monographers, since genera referred by Schinz to subtribes Amaranthinae and Achyranthinae were substantially rearranged. In the present paper the classification of Schinz is used, with the exception that, following Mears, tribe Brayulineeae is included within the Gomphreneae.

The Amaranthaceae belong to the order Centrospermae (Caryophyllales, Chenopodiales), one of the most natural and clearly defined orders of flowering plants. There has been spirited debate, however, over the importance that should be given to the betalain or anthocyanin pigments. Mabry places all the families with betalain pigments in suborder Chenopodiineae, and the Caryophyllaceae and Molluginaceae, both of which have anthocyanin pigments, in suborder Caryophyllineae. Cronquist does not subdivide the order, while Thorne recognizes three suborders: Chenopodiineae (betalains plus anomalous secondary thickening from successive cambia), Portulacineae (betalains, no anomalous secondary thickening), and Caryophyllineae (anthocyanins and anomalous secondary thickening). In Takhtajan's most recent classification scheme, order Caryophyllales is divided into three suborders: Phytolaccineae (all but two betalain families), Caryophyllineae (anthocyanin families), and Chenopodiineae (Chenopodiaceae and Amaranthaceae—both betalain families).

The Amaranthaceae are very closely allied to the Chenopodiaceae (the two were united by Baillon), and they share a number of characteristics: anomalous secondary thickening, generally small flowers, a perianth of tepals in one whorl, pollen characters (see Nowicke, and Skvarla & Nowicke), a syncarpous and superior gynoecium usually with one ovule, distinctive centrospermous embryology, basal or free-central placentation, betalain pigments (see Mabry), and P-type form (c) sieve-element plastids (see Behnke). The Amaranthaceae are distinguished from the Chenopodiaceae by the dry, scarious bracts, bractlets, and tepals, and by the androecium usually with connate filaments and frequently with pseudostaminodia.

A new character that has been of significance in the delimitation of the Centrospermae is the type of plastid found in sieve elements. In most plants, these plastids accumulate starch; however, in all the families assigned to the Centrospermae by Mabry (1977), and only in these families, the sieve elements accumulate protein in ring-shaped bundles of filaments. The plastids of the Amaranthaceae and Chenopodiaceae lack the central crystalloid structures that are found in the other centrospermous families.

The pollen of all Amaranthaceae studied thus far (Handro, Livingstone *et al.*, Martin & Drew, Nair & Rastogi, Nowicke, Rădulescu, Riollet & Bonnefille, Skvarla & Nowicke, Tsukada, Vishnu-Mittre, and Zandonella & Lecocq) is pantoporate and mostly spherical. The pores are covered with various amounts of ektexine, which is developed into protruding stellate structures in *Papulia*. There are two basic subtypes of pollen, corresponding to the two subfamilies. The pollen of subfamily Amaranthoideae has a spinulose

and tubuliferous/punctate ektexine. (According to Nowicke, similar pollen is found in the Caryophyllaceae, Chenopodiaceae, Dysphaniaceae, and Phytolaccaceae.) In subfamily Gomphrenoideae, the pores are deeply recessed, giving the pollen a reticulate or polyhedral appearance. There is considerable variation in pollen morphology within both subfamilies, and it is likely that this variation will prove to have some taxonomic significance.

Chromosome numbers have been reported for only about 20 of the ca. 65 genera of Amaranthaceae, and the vast majority of counts are of species of *Amaranthus*. Based on this small sample, the family has a wide variety of base chromosome numbers: 6, 7, 8, 9, 10, and 13—plus some multiples and combinations of these. This is in contrast to the Chenopodiaceae, which have a uniform base number of 9. Numerous ploidy levels from diploid to duodecaploid are also known in the Amaranthaceae. Several different base numbers are frequently reported within the same genus (see discussion under *Amaranthus*), some species have cytological races, and in *Digera arvensis* Fôrskal there are different chromosome numbers in different nuclei of pollen mother cells (Desai, 1971), which may account for the different chromosome numbers reported for the species. It seems that much remains to be learned about the cytology of the Amaranthaceae and that detailed studies at the generic or family level would be worthwhile.

Despite the weedy character of many members of the family, the Amaranthaceae are of considerable use to man. The seeds of *Amaranthus* species have been used as pseudo-cereal grains in many parts of the world, and a number of domesticated races have been developed in Central and South America. Species of *Amaranthus* and *Celosia* are also widely used as potherbs. Some species of *Amaranthus*, *Alternanthera*, and *Iresine* have colorful foliage and are cultivated as ornamentals, and species of *Gomphrena* and *Celosia* are grown for their showy inflorescences.

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KEY TO THE GENERA OF AMARANTHACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *annual or perennial herbs; leaves alternate or opposite, simple, mostly entire, exstipulate; inflorescences of cymes grouped in terminal and/or axillary spikes, panicles, heads, clusters, or racemes, bracteate and usually bibracteolate; flowers small, regular, perfect, or imperfect and the plants monoecious or dioecious; tepals usually 4 or 5, free or basally connate, equal to unequal, imbricate, scarious, chartaceous, or indurate; stamens usually 4 or 5(3), opposite the tepals; filaments free or more commonly basally connate into a cup or tube with the free portions often alternating with variously shaped pseudostaminodia; anthers dorsifixed, introrse, with 2 or 4 locules; ovary superior, 1-loculate and 2- or 3-carpellate; ovules 1 (or numerous), predominantly campylotropous, the placentation basal; fruit generally a dry, dehiscent or indehiscent utricle; seeds small, shiny, lenticular to subglobose or subreniform, the embryo peripheral around the mealy perisperm.*

A. Leaves alternate.
  B. Flowers perfect; ovaries with several ovules, the fruits with several seeds. . . . . 1. *Celosia.*
  B. Flowers imperfect; ovaries with one ovule, the fruits with one seed. . . . . 2. *Amaranthus.*

A. Leaves opposite.
  C. Flowers imperfect; inflorescences terminal, diffuse, open panicles. . . . . 9. *Iresine.*
  C. Flowers perfect; inflorescences terminal and/or axillary spikes, heads, or glomerules.
    D. Inflorescences terminal, simple or compound, elongate spikes.
      E. Inflorescences mostly interrupted, compound spikes; tepals united into a lanate perianth tube bearing lateral crests or spines. . . . . 6. *Froelichia.*
      E. Inflorescences mostly simple spikes with the flowers progressively farther apart toward the base; tepals free or basally connate, ± glabrous, without lateral crests or spines. . . . . 3. *Achyranthes.*
    D. Inflorescences axillary and/or terminal heads, glomerules, or short, condensed spikes.
      F. Inflorescences axillary glomerules or short spikes.
        G. Indumentum of stellate trichomes. . . . . 5. *Tidestromia.*
        G. Indumentum, when present, of simple trichomes.
          H. Inflorescences few-flowered axillary glomerules; pseudostaminodia absent. . . . . 4. *Guilleminea.*
          H. Inflorescences short, axillary spikes; pseudostaminodia present. . . . . 7. *Alternanthera.*
      F. Inflorescences terminal heads or headlike spikes.
        I. Inflorescences immediately subtended by one or more leaves.
          J. Leaves fleshy, linear to narrowly obovate, sessile, glabrous except in the axils. . . . . 10. *Philoxerus.*
          J. Leaves not fleshy, ovate, shortly petiolate, long-pilose at least below and on the margins. . . . 8. *Gomphrena.*
        I. Inflorescences not subtended by leaves. 7. *Alternanthera.*

Subfamily AMARANTHOIDEAE

Tribe CELOSIEAE Endl.

1. **Celosia** Linnaeus, Sp. Pl. **1:** 205. 1753; Gen. Pl. ed. 5. 96. 1754.

Annual or perennial herbs, often woody below [or shrubs or small trees]; stems slender to stout, usually much branched, often over 1 m. tall or long, glabrous [or pubescent], erect or scandent. Leaves alternate, petiolate, often decurrent, entire [or lobed], the blades lanceolate, ovate, deltoid, or linear, symmetrical or asymmetrical; 2 small, falcate leaves (often mistaken for stipules) sometimes in the axils of normal leaves. Inflorescences terminal and also often axillary, sessile or pedunculate, solitary or clustered, continuous or interrupted spikes or fascicles [rarely cymes], usually fasciated in cultivated forms. Flowers perfect, subtended by 1 bract and 2 bractlets, brownish to (especially in cultivated forms) various shades of red, pink, yellow, purple, white, or silver. Tepals 5, distinct, ± equal, glabrous, scarious, striate nerved, persistent and erect in fruit, imbricate in aestivation. Stamens 5; filaments united below into a membranaceous cup, the free portions subulate or filiform; pseudostaminodia usually absent but sometimes present and dentate, alternating with the free portions of the filaments; anthers dorsifixed, introrse, with 4 locules and 2 lines of dehiscence. Style 1, short, elongate [or nearly absent], sometimes indurated, terminated by 2 or 3 capitate or subulate stigmatic lobes; ovary ovoid, subglobose, or cylindrical, sessile, unilocular; ovules usually 2 to many, campylotropous, inserted at the tip of elongate funiculi attached to a basal placenta. Fruit a subglobose or ovoid, membranaceous, usually centrally circumscissile utricle. Seeds 2 to many, erect, lenticular, shiny, smooth; embryo annular around the mealy perisperm, the cotyledons linear, the radicle inferior. LECTOTYPE SPECIES: *C. argentea* L.; see P. C. Standley, N. Am. Fl. **21:** 96. 1917, and also A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 135. 1929. (Name from Greek *keleos,* burning, alluding to the color and/or appearance of the inflorescence; an ancient name adopted by Linnaeus for this genus.) — COCKSCOMB.

Perhaps 65 species, mostly of the tropics and subtropics of the Americas and Africa. Only two species are indigenous to the continental United States, while one or two other species, depending on taxonomic concepts, have been introduced and have escaped from cultivation. *Celosia nitida* Vahl, a perennial herb with a woody taproot and slender, erect, often scandent stems, occurs in coastal sand dunes and hammocks near the seashore in southern peninsular Florida and the Florida Keys, as well as in Texas, the West Indies, Mexico, and Central and South America. *Celosia Palmeri* S. Watson, a much-branched, low shrub, reaches southern and western Texas; it also occurs in northeastern Mexico.

One taxonomic complex includes *Celosia argentea* L., a wild species, and the cultivated "cockscomb," which is variously treated as a distinct species

(*C. cristata* L.), a variety (*C. argentea* var. *cristata* (L.) O. Kuntze), or a form (*C. argentea* f. *cristata* (L.) Schinz). Both taxa have escaped sporadically in our area, but neither seems to have become strongly established.

Celosia argentea was perhaps originally native to India, although it is very widespread today, either as a weed or as an escape from cultivation, from the tropics to warm-temperate regions of both hemispheres. Throughout most of its present range the species is an octoploid with $2n = 72$, although a tetraploid race (races?) has been found in eastern, western, and central India (Khoshoo & Pal, Behera & Patnaik, Desai, the last two under family references). Cultivated cockscomb thus far appears to be uniformly tetraploid with $2n = 36$. The unusual occurrence of a tetraploid cultivated species and a closely related, predominantly octoploid species has caused some interesting speculation. Grant, unaware of the tetraploid race of *C. argentea*, postulated—on the basis of cytological and morphological observations on *C. argentea* and cockscomb, F_1 and F_2 hybrids between them, and an autoallopolyploid—that *C. argentea* is an allopolyploid that arose between cockscomb and some unknown species. This hypothesis was questioned by van Steenis (see Backer, family references); and Khoshoo & Pal, after cytological and breeding studies on cockscomb and tetraploid plants of *C. argentea*, argued that cockscomb had its origin in selections made long ago from tetraploid forms of *C. argentea*. Grant presents good arguments for maintaining *C. argentea* and *C. cristata* as distinct species (a course followed in *Hortus Third*, p. 241. 1976), while Khoshoo & Pal think that the close genetic relationship within the complex, as revealed in their crossing experiments, is best reflected in a taxonomic scheme that recognizes only one species, *C. argentea*, with several varieties.

Cockscomb, which has the longest history of cultivation of any fasciated plant, is widely grown as an ornamental throughout much of the world for its colorful, fasciated inflorescences that come in many shades of yellow and red to white, orange, or deep purplish red. There are two basic inflorescence types (plumose and widely convoluted combs); within each type, the forms breed true. *Celosia argentea* is also a popular vegetable in Africa.

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Tribe AMARANTHEAE

2. **Amaranthus** Linnaeus, Sp. Pl. **2:** 989. 1753; Gen. Pl. ed. 5. 427. 1754.[2]

Annual [very rarely perennial], often weedy, robust herbs, sometimes woody below; stems erect, ascending, or infrequently decumbent, simple or much branched from the base, unarmed or rarely with a pair of spines at the bases of the leaves, sometimes striate and/or fleshy, green to reddish or whitish, coming from a stout taproot. Leaves alternate, entire or undulate, rhombic, lanceolate, ovate, oblanceolate, obovate, or rarely spathulate and emarginate, sometimes ± fleshy, green to reddish or yellowish, the midrib often excurrent and sometimes spinescent; petioles usually elongate; stipules absent. Inflorescences dense terminal and/or axillary compound dichasia arranged in spikes, thyrses, panicles, or glomerules, the axis sometimes greatly thickened, the inflorescence units often subtended by reduced leaves; each dichasium subtended by a persistent, usually spine-tipped bract. Flowers small, greenish or reddish, imperfect and the plants either monoecious or dioecious. Tepals usually 3–5, or absent or rudimentary in carpellate flowers, distinct,

[2] See Sprague regarding the spelling *Amaranthus* vs. *Amarantus.*

membranaceous, ± equal or the outer exceeding the inner, glabrous, the midrib faint to broad, usually excurrent and often spinescent. Stamens 3–5, absent in carpellate flowers; filaments free to the base; pseudostaminodia absent; anthers dorsifixed, introrse, with 4 locules and 2 lines of dehiscence. Style short or absent; stigmas 2 or 3, subulate, persistent; ovary ovoid, absent in staminate flowers; ovule 1, erect, the micropyle inferior, the funiculus short. Utricle 1-seeded, 2- or 3-beaked, membranaceous and circumscissile, irregularly dehiscent, or indehiscent. Seed lenticular to subglobose, smooth, shining; embryo coiled into a ring around the perisperm, the radicle inferior. (Including *Acnida* L.) LECTOTYPE SPECIES: *A. caudatus* L.; see N. L. Britton & A. Brown, Illus. Fl. No. U. S. Canada. ed. 2. **2:** 1. 1913; also A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 188. 1929. (Name from Greek *amarantos*, unfading, evidently referring to the persistent, unwithering tepals; this name was applied by Ovidius and Plinius to *Celosia* and by Dioscorides and Galenus to *Helichrysum* (Compositae). — AMARANTH.

Perhaps 60 species now nearly cosmopolitan in distribution, particularly abundant as weeds in cultivated fields and other disturbed sites; the great majority of species originating in the New World. Since many species are weedy and the seeds are often carried about by man, both intentionally and inadvertently, it is difficult to say exactly how many species are indigenous or naturalized in any given area. About 26 species are native to America north of Mexico, 10 of them to the eastern United States. Approximately 13 species are introduced into the eastern United States from the western United States, Mexico, Central America, and South America. Some of these introductions are local and possibly only ephemeral, while others are now very common and widespread.

The species of *Amaranthus* are sometimes difficult to distinguish, especially for one not familiar with the group. The flowers are small, but floral characters are essential; young plants may not have mature fruits, which are sometimes needed; there are few distinguishing features for staminate plants of species of subg. ACNIDA; and a number of characters are qualitative. Also, some taxonomists consider amaranths mere weeds and do not take the time to examine them carefully. In any case, herbarium specimens of the genus are frequently misidentified. Collectors also tend to ignore the genus, presuming that the species are everywhere and have surely been collected from a given area before. As a result, it is likely that the geographic distributions for species of *Amaranthus* given in various floras and manuals are incomplete and/or inaccurate.

The genus can be subdivided into two subgenera: AMARANTHUS (plants monoecious) and ACNIDA (L.) Aellen ex K. R. Robertson[3] (plants dioecious).

[3] **Amaranthus** subgenus **Acnida** (L.) Aellen ex Robertson, comb. nov. Basionym: *Acnida* Linnaeus, Sp. Pl. **2:** 1027. 1753; Gen. Pl. ed. 5. 427. 1754. TYPE SPECIES: *Acnida cannabina* L. = *Amaranthus cannabinus* (L.) Sauer. Aellen (1959, pp. 467, 474) did not give a full and complete reference for the basionym, as required after 1 January 1953 by Article 33 of the International Code of Botanical Nomenclature.

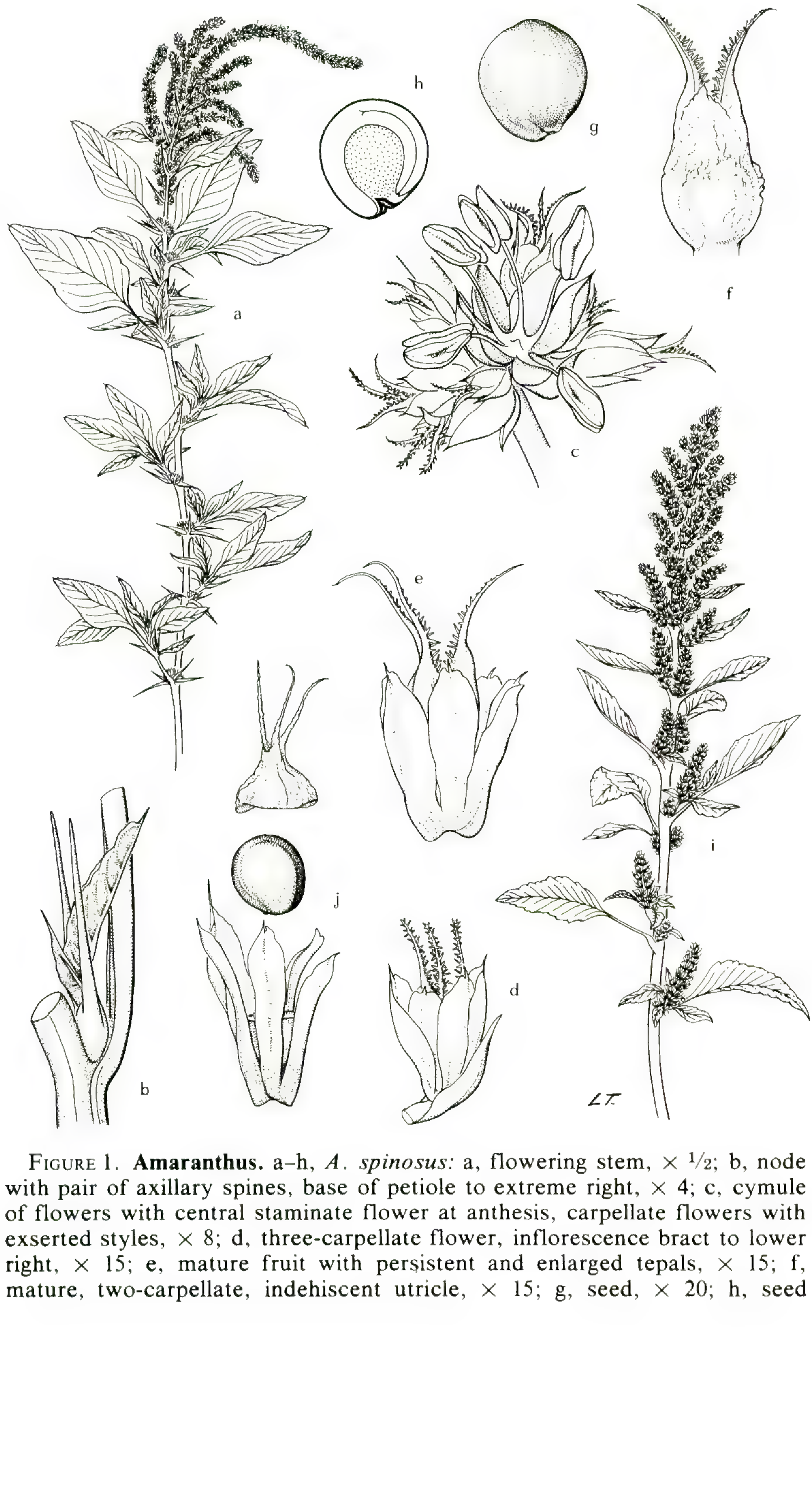

FIGURE 1. **Amaranthus.** a–h, *A. spinosus:* a, flowering stem, × 1/2; b, node with pair of axillary spines, base of petiole to extreme right, × 4; c, cymule of flowers with central staminate flower at anthesis, carpellate flowers with exserted styles, × 8; d, three-carpellate flower, inflorescence bract to lower right, × 15; e, mature fruit with persistent and enlarged tepals, × 15; f, mature, two-carpellate, indehiscent utricle, × 15; g, seed, × 20; h, seed

Subgenus AMARANTHUS is composed of two sections: AMARANTHUS (sect. *Amaranthotypos* Dumort.; "*Paniculati*" of Small), with large terminal inflorescences and circumscissilely dehiscent fruits; and BLITOPSIS Dumort. (group "*Crassipes*" of Small), with axillary flower clusters and mostly indehiscent fruits. Kowal (1955) proposed a third section for *A. gracilis* Desf. (= *A. viridis*) and *A. acutilobus* Uline & Bray, but no Latin diagnosis accompanied the name, which is thus invalid.

Perhaps only two species of sect. AMARANTHUS are native to the southeastern United States: *A. hybridus* L. and *A. retroflexus* L. According to Sauer (1967), both of these were riverbank pioneers in eastern North America (and westward and southwestward). They are now extremely abundant weeds in agricultural fields and waste places and, like most of our common weeds, are often taken for exotic species. *Amaranthus spinosus* L., originally of the New World tropical lowlands (Sauer, 1967), is now a pantropical weed and is common in our area, especially in barnyards and other areas where livestock is raised. A number of other species of sect. AMARANTHUS have been introduced into our area but have not yet become widely established. These include *A. hypochondriacus* L. (a pseudo-grain crop of southwestern North America derived mainly from *A. Powellii*), *A. cruentus* L. (also a pseudo-grain crop from Mexico or Guatemala, probably derived from *A. hybridus*), *A. caudatus* L. (an Andean pseudo-grain crop perhaps derived from *A. quitensis* HBK.), *A. Powellii* S. Watson (native to cordilleran North and South America), and *A. viridis* L. (a pantropical weed; incl. *A. gracilis* Desf.). Because of the weedy nature of the species of sect. AMARANTHUS, geographic ranges are not given here, since they are difficult to give precisely, being subject to frequent extensions and/or local eradications.

One, or possibly two, species of sect. BLITOPSIS are indigenous to our area, and others are introduced. *Amaranthus pumilus* Raf. is local on beach dunes from Nantucket and Martha's Vineyard, Massachusetts, southward along the coast to South Carolina. *Amaranthus polygonoides* L., a rather weedy plant of sandy soil and waste ground, occurs sporadically from Florida to Texas, and in Mexico, northern South America, the Bahamas, and the West Indies; it is not clear whether this species is indigenous in the Southeast. *Amaranthus crassipes* Schlecht., supposedly introduced from tropical America, is found along the Gulf coast from Florida to Texas; it also occurs in the Bahamas, the West Indies, and northern South America and has been introduced at seaports and along railroad tracks in the eastern United States, including Aiken Co., South Carolina. Two other species of this section are introduced weeds in our area: *A. albus* L. (*A. graecizans* of American authors, not L.), tumbleweed, originally native to the prairies and plains of central North America, but now widespread throughout the continent;

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in section, perisperm stippled, × 20. i, j, *A. retroflexus:* i, upper part of small plant with flowers and fruits, × 1/2; j, mature, circumscissilely dehiscent utricle (pyxis) with lid at top, seed in middle, and persistent tepals and base of fruit below, × 12.

and *A. blitoides* S. Watson (also *A. graecizans* of American authors, not L.),[4] native to western and central North America but now widespread in the eastern part of the continent. *Amaranthus Blitum* L. (*A. lividus* L.) has been reported from North Carolina and Florida. (See Fillias *et al.* and Brenan for differing views on the name of this species.)

As delimited by Standley (1917, family references), Reed (1969, family references), and others, *Acnida* included those dioecious species with carpellate flowers lacking a well-developed perianth. (Dioecious species with an evident perianth were included in *Amaranthus*.) Sauer (1955) pointed out that the perianth character is inconsistent and that "the dioecious habit, which is extremely constant, is the only morphological character distinguishing this group [*Acnida*] as a whole from all the monoecious amaranths. . . . The balance of the evidence seems to show that the affinity between *Acnida* and *Amaranthus* is too great to justify maintaining them as separate genera. . . ." Sauer also included the monotypic *Acanthochiton Wrightii* Torrey of the southwestern United States and adjacent Mexico, which has broad, foliaceous bracts on the carpellate inflorescences, within *Amaranthus* as *A. Acanthochiton* (Torrey) Sauer. Although Sauer (1957) did not propose a formal taxon for the dioecious amaranths, he did consider them to be a group of related species, in the present paper placed in subgenus ACNIDA.

Subgenus ACNIDA, composed of ten species, is restricted to the New World, primarily North America, Mexico, and the Greater Antilles. Nearly all species occur in wet habitats, and four are maritime. The group has been studied extensively by Sauer (1955, 1957, 1972). Seven species occur in the southeastern United States (see distribution map in Sauer, 1957). *Amaranthus floridanus* (S. Watson) Sauer (*Acnida floridana* S. Watson), endemic to Florida, occurs mostly on coastal dunes and beaches on the eastern and western shores of peninsular Florida. *Amaranthus australis* (A. Gray) Sauer (*Acnida australis* A. Gray; including *Acnida alabamensis* Standley and *Acnida cuspidata* Bert. ex Sprengel) is found in wet areas near both fresh and salt water over much of Florida and ranges westward and southward along the coasts of the Gulf of Mexico and the Atlantic Ocean to Texas, Mexico, Venezuela, Surinam, and Brazil; it also occurs on the Greater Antilles. Individuals of *A. australis*, which is presumably annual, can become amazingly tall, and there are reports of plants up to 9 m. high (see Sauer 1955, 1972). *Amaranthus cannabinus* (L.) Sauer (*Acnida cannabina* L.), a plant of the Atlantic tidewater zone, ranges from southern Maine to northernmost Florida; it also extends inland along the Hudson and Delaware rivers. *Amaranthus tuberculatus* (Moq.) Sauer (*Acnida altissima* Riddell, *Acnida subnuda* (S. Watson) Standley) is widespread in the northeastern and midwestern United States but is absent from most of the Mid-Atlantic and Southeastern states; in our area it is found in western

[4]This species is called *A. graecizans* in many floras of the eastern United States, following Fernald (1945); but Sauer & Davidson (family references) maintain that this name is properly applied to an Old World species and that *A. blitoides* is the correct name for the plants in North America. This latter nomenclature is also used by Aellen and by Tutin (see family references).

Alabama and Tennessee and in eastern Louisiana and Arkansas. *Amaranthus rudis* Sauer (*Amaranthus tamariscinus* of authors, not Nutt.; see Sauer, 1972) occurs primarily in the midwestern United States from North Dakota eastward to Indiana and southward to eastern Tennessee, Mississippi, and Texas. *Amaranthus Palmeri* S. Watson was originally a plant of southwestern North America but is now introduced in Florida, South Carolina, Louisiana, and several Midwestern and Northeastern states; according to Sauer (1955), this probably is the weediest of the dioecious amaranths. *Amaranthus Greggii* S. Watson is known from our area only by one collection (*Thieret & Reese 10028*), from Cameron Parish, Louisiana, which was made a year after Hurricane Clara, and Sauer (1972) suggests that the population was only ephemeral. This species occurs in pioneer beach vegetation from the Yucatan Peninsula northward along most of the Texas coastline.

In the genus there are two basic chromosome numbers, 16 and 17, evidently distributed without taxonomic significance. Nearly all species examined thus far are diploid with $2n = 32$ or 34; but *Amaranthus dubius* Mart. ex Thell., *A. giganteus* Koenig, and *A. caturtus* Heynh. are reported to be tetraploids with $2n = 64$.

Species of *Amaranthus* can be prolific seed producers. In a short note, G. N. Jones passed on the unpublished observations of C. F. Hottes that a single plant of *A. retroflexus* growing near Urbana, Illinois, in 1895 produced an estimated 2,359,000 seeds, and one of *A. albus* produced approximately 1,606,000.

Three (as delimited by Sauer) New World species of *Amaranthus* were domesticated as pseudo-grain crops before the Spanish Conquest: *A. hypochondriacus* in northwestern and central Mexico, *A. cruentus* in southern Mexico and Central America, and *A. caudatus* in the Andean highlands of South America. While the seeds of all wild and cultivated nongrain species of *Amaranthus* are blackish, those of species grown for their seeds are pale ivory; the oldest records for pale amaranth seeds are of *A. cruentus* from Coxcatlán Cave, near Tehuacán, Puebla, Mexico, at levels dated at about 4000 and 2500 B.C. At the time of the Conquest, *A. hypochondriacus* was a major grain crop in central Mexico. The plant also had considerable religious significance, since idols used in the most important ceremonies were made from the seeds. Because of this pagan usage, the cultivation of the "grain" amaranths was suppressed under Christianity, and today they are grown only vestigially in this hemisphere. The pseudo-grain amaranths, especially *A. hypochondriacus*, were carried very early to the Old World (early botanists considered them an Old World crop), and they are rather commonly cultivated there today, especially in the Himalayan region. The seeds of pseudo-grain amaranths are used in several ways: parched and milled into flour, cooked for gruel, popped and molded into cakes with syrup, or powdered and made into a drink. The nutritional value of the seeds is very high; of special importance is the high level of lysine, an essential amino acid in which most grains are deficient. Grain amaranths are considered a crop that could potentially be further developed through a breeding program to augment the few major grains suitable for developing countries.

Certain highly red-pigmented forms of *Amaranthus cruentus* were selected by Indians, and a dye used to color ceremonial wafers was extracted from the plants. Today, these red forms are cultivated in much of the world as potherbs and ornamentals. Red-pigmented forms of *A. caudatus* are also grown as ornamentals. *Amaranthus cruentus* is well known as a vegetable in Africa, as *A. tricolor* L. (*A. gangeticus* L.) is in Asia. *Amaranthus caudatus*, *A. inamoenus* Willd., *A. paniculatus* L., *A. tricolor*, and *A. viridis* are used as vegetables in China.

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3. **Achyranthes** Linnaeus, Sp. Pl. **1:** 204. 1753; Gen. Pl. ed. 5. 96. 1754, "*Achyrantes.*"

Annual or perennial herbs, sometimes suffrutescent at the base, with erect, ascending, or decumbent, simple to much-branched, glabrous to tomentose or sericeous, terete or quadrangular stems. Leaves opposite, petiolate [or sessile], the blades entire, elliptical to ovate, obovate, or orbicular. Inflorescences terminal and axillary, many flowered, mostly elongate, often interrupted spikes or panicles, only a few flowers open at the same time; bracts membranaceous, the bracteoles long-aristate and spinose. Flowers perfect, whitish, greenish, pinkish, or reddish, often becoming deflexed in age. Tepals 4 or 5, basally connate, coriaceous, becoming indurated in fruit, the segments narrow, nearly equal or not, acute, acuminate, or awned, pungent or not in fruit, glabrous or pubescent, with one or more prominent veins. Stamens 5, much shorter than tepals, the filaments alternating with pseudostaminodia, all connate below into a cup; filaments filiform; pseudostaminodia erose to laciniate, often with a prominent dorsal scale; anthers with 4 locules and 2 lines of dehiscence. Style 1, elongate, filiform; stigma 1, small, capitate; ovary obovoid, turbinate, or ovoid, slightly compressed, glabrous; ovule 1, pendulous from the tip of an elongate funiculus, the micropyle superior. Fruit an indehiscent, ovoid or obovoid, truncate or apically depressed, membranaceous utricle enclosed by the indurated tepals, falling off with the perianth and bracteoles; seeds obovoid or ovoid, smooth, inverted; embryo peripheral, surrounding the mealy perisperm, the cotyledons linear or lanceolate, flattened, the apices incurved from the erect radicle. (*Centrostachys* Wall. in Roxb.; not *Achyranthes* sensu Standley, Jour. Wash. Acad. Sci. **5:** 72. 1915, and N. Am. Fl.) LECTOTYPE SPECIES: *A. aspera* L.; see A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 135. 1929, and A. A. Bullock, Kew Bull. **1957:** 73. 1957. (Name from Greek *achyron*, chaff, and *anthos*, flower.)

About 8–12 species mostly in the tropics, subtropics, and warm-temperate zones of the Old World (3 species occur in Japan), with *Achyranthes aspera* very widespread in both the Old and New Worlds. Townsend (1974b, family references) noted that *Achyranthes* is "a very difficult genus taxonomically, greatly in need of cytological and experimental investigation; there appear to have been a number of geographical races of, in particular, *A. aspera;* these, getting about as weeds, have probably interbred with local populations. The result has been a welter of forms virtually defying taxonomic treatment."

There has been considerable nomenclatural confusion with regard to this genus, largely because Standley changed existing generic concepts by designating *Achyranthes repens* L. as the lectotype species of *Achyranthes* and

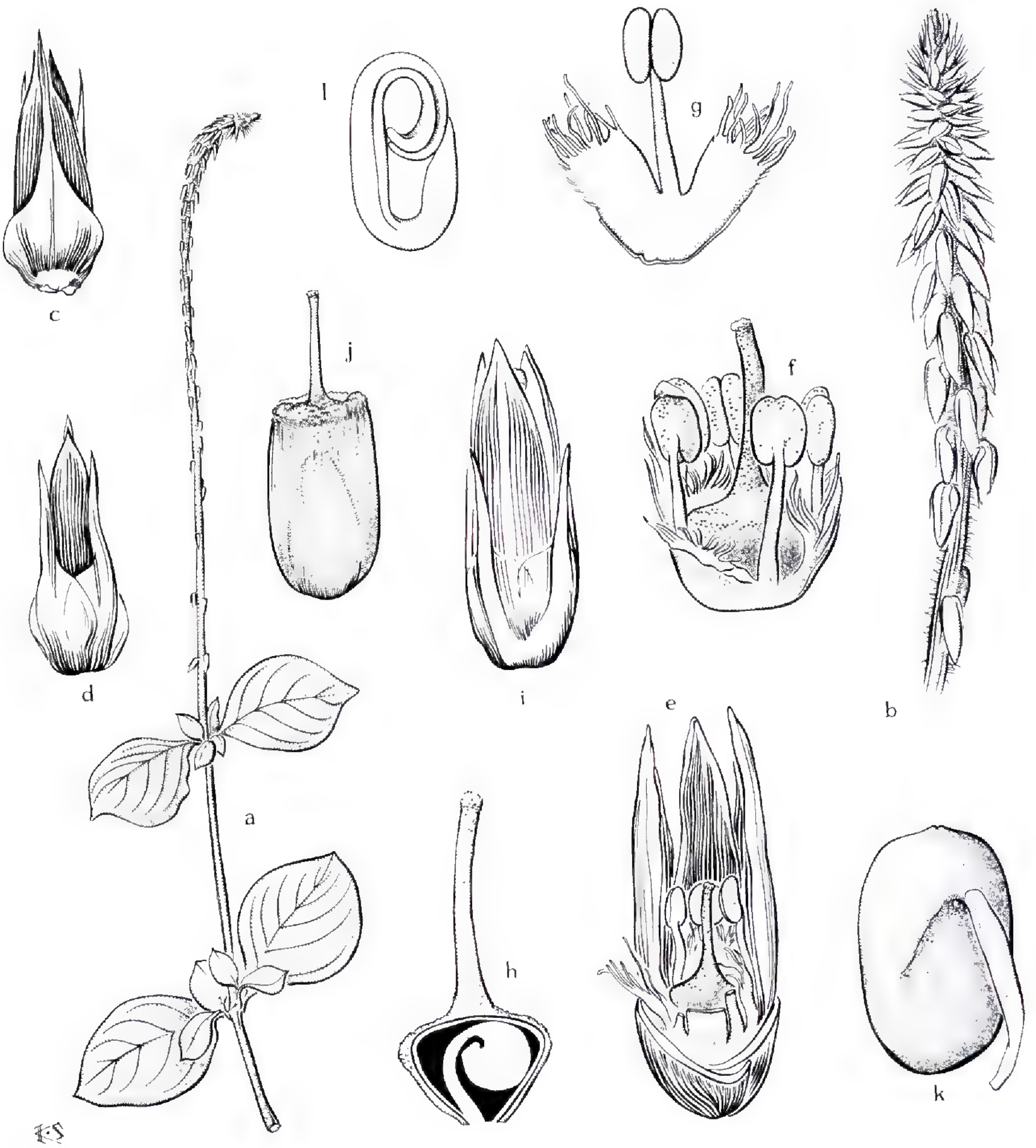

FIGURE 2. **Achyranthes.** a–l, *A. aspera:* a, upper part of flowering and fruiting stem, × 1/2; b, tip of same, × 2; c, abaxial side of inflorescence bract and, in its axil, a flower, × 10; d, adaxial side of same showing lateral, spinescent bracteoles, × 10; e, flower with two tepals, two stamens, and pseudostaminode partly removed, × 12; f, androecium and gynoecium removed from flower—note pseudostaminodia alternating with stamens, × 20; g, adaxial side of part of androecial cup with one stamen and two pseudostaminodia, × 20; h, gynoecium, part of ovary wall removed to show ovule suspended from tip of elongate funiculus, × 25; i, mature fruit surrounded by accrescent, indurated tepals and spiny, lateral bracteoles, × 10; j, mature utricle, × 12; k, seed with persistent funiculus, tip of radicle visible through thin seed coat, × 15; l, embryo removed from seed, × 12.

transferring species previously referred to *Alternanthera* to *Achyranthes;* species that had been included in *Achyranthes* were placed by Standley in *Centrostachys* Wall. However, Bullock demonstrated that Standley's lectotypification of *Achyranthes* was incorrect and that the lectotype species should be *A. aspera* L. This essentially returned the concepts of these genera to those that had existed earlier. *Centrostachys* now includes only *C. aquatica* (R. Br.) Wall. ex Moq., which is frequently included within *Achyranthes.*

Achyranthes aspera L. (*Centrostachys aspera* (L.) Standley, *C. indica* (L.) Standley), $2n = 42$, occurs mostly in waste ground and old fields from southern Florida to southern Alabama and Texas; it is a pantropical weed, now being found in the West Indies and Central America, as well as in the Old World from the south coast of Europe to Africa and southern Asia. This is a very variable species in which numerous subspecific taxa have been proposed. Two leaf forms occur in our area: the one ovate to broadly ovate, acuminate, the other orbicular to obovate-orbicular, rounded and apiculate. The first has been called var. *aspera,* the second var. *indica* (L.) Miller. However, Cavaco (family references) concluded that the type material of *A. aspera* is from Ceylon and that the plants that have been called var. *indica* must now be referred to var. *aspera.* Townsend (1974a, family references) adopted the name *A. aspera* var. *pubescens* (Moq.) Townsend for the taxon previously known as var. *aspera.*

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Subfamily GOMPHRENOIDEAE Schinz

4. **Guilleminea** Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. **6:** ed. fol. 34, ed. quarto. 40. *pl. 518.* 1823; not *Guilleminia* Necker, 1790, *nomen illegit.*

Perennial herbs [rarely suffrutescent or caespitose] with numerous, much-branched, prostrate or ascending stems radiating from a stout taproot. Leaves opposite, entire, linear to lanceolate, spathulate, or ovate, of three types—large, elongate, persistent [or withering] basal leaves in a rosette, moderately large cauline leaves [members of each pair unequal], and small leaves subtending each inflorescence; blades long-tapering at base into a winged petiole. Inflorescences much-condensed spikes, rarely of solitary flowers, in axillary glomerules; each flower subtended by 2 bracts and 1 bractlet, all subequal, persistent, and membranaceous. Flowers perfect, minute, ± sessile. Tepals 5, ± equal, free [or the bases connate into a cup], abaxially lanate. Stamens 5; filaments connate below into a tube, the tube free from [or adnate to] the calyx; anthers with 2 locules and 1 line of dehiscence; staminodia and pseudostaminodia absent. Style 1, usually short; stigma capitate, inconspicuously bilobed; ovary compressed; ovule solitary, anatropous, pendulous from the tip of a long funiculus, the micropyle superior. Fruit a small, membranaceous, indehiscent utricle. Seed nearly filling the fruit, lenticular-orbicular, shiny reddish brown; embryo annular, surrounding the central, mealy perisperm, the radicle superior. (*Brayulinea* Small; including *Gossypianthus* Hooker, see Mears.) Type species: *G. illecebroides* HBK. =

G. densa (Willd. ex Roemer & Schultes) Moq.[5] (Named for Antoine Guillemin, 1796–1842, French botanist, author, and explorer; in the dedication of the genus, particular mention was made of Guillemin's then unpublished observations on the Gentianaceae.) — COTTONFLOWER.

According to the latest revision (Mears), five species and ten varieties in two subgenera of the south-central and southwestern United States, Mexico, Hispaniola, Cuba, Colombia, Ecuador, Peru, Bolivia, Paraguay, Uruguay, and Argentina. The genus is represented in our area only by the occasional occurrence in Arkansas of *Guilleminea lanuginosa* var. *tenuiflora*.

Guilleminea lanuginosa (Poiret) Hooker f. is a variable species that ranges from western Arkansas and central Oklahoma through much of Texas to southwestern Chihuahua and central Tamaulipas; it also occurs in Hispaniola. Four varieties, distinguished mostly by the density of trichomes and the shape and size of the basal and cauline leaves, were recognized by Mears. Varietas *tenuiflora* (Hooker) Mears, a fairly large, often glabrous plant with ascending stems and linear radical leaves 40–90 mm. long, occurs in prairies and savannas from western Arkansas and central Oklahoma southward to southern Texas and Tamaulipas.

Guilleminea Brittonii (Standley) Mears, a Cuban endemic, is closely related to *G. lanuginosa*. Most authors have considered these two to comprise *Gossypianthus* Hooker, which was distinguished from *Guilleminea* by the persistent, rather than withering, basal leaves, and by the androecial tube being free from, instead of adnate to, the calyx. These characters are evidently subject to variation, however, and Mears considered *Gossypianthus* to be a subgenus of *Guilleminea*. The other species of *Guilleminea*, all belonging to subg. GUILLEMINEA, are *G. densa* (Willd.) Moq. (Oklahoma to Oaxaca, and disjunctly from southern Colombia to Argentina and Uruguay), *G. australis* (Griseb.) Hooker f. (Jujuy Prov., Argentina, and western Paraguay), and *G. elongata* Mears (Uruguay). In the checklist of Amaranthaceae in Kartez & Kartez (family references), of which the Gomphrenoideae were reviewed by Mears, *Gossypianthus* is again treated as distinct from *Guilleminea*.

Guilleminea has usually been referred to tribe Brayulineeae Standley, along with *Tidestromia*. With the inclusion of *Gossypianthus*, Mears considered *Guilleminea* to be a member of tribe Gomphreneae Schinz.

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[5]Reed cites "*Paronychia lanuginosa* Poir." as the type of *Guilleminea*, but this is the basionym of the correct specific name for *Gossypianthus rigidiflorus* Hooker, which is the type species of the segregate genus *Gossypianthus* Hooker (= *G. lanuginosa* (Poiret) Hooker f. in Bentham & Hooker var. *rigidiflora* (Hooker) Mears).

5. **Tidestromia** Standley, Jour. Wash. Acad. Sci. **6:** 70. 1916.

Annual [or perennial] herbs, sometimes suffruticose at base; stems much branched, prostrate or ascending, radiating from a slender to thick caudex and taproot [or from horizontal rhizomes] ; indumentum of stellate or branched trichomes. Leaves opposite, entire, petiolate, decreasing in size toward tips of branches, the blades broadly ovate, orbicular, or spathulate with truncate to tapering bases and rounded to slightly acute apices; bases of the uppermost leaves ± connate and indurated, forming an involucre. Inflorescences axillary glomerules, bracteate and bibracteolate, the bracts and bracteoles hyaline and pubescent. Flowers perfect, minute. Perianth segments 5, distinct, the outer 3 wider than the inner 2, membranaceous, glabrescent or villous. Androecium of 5 hypogynous stamens; filaments connate below into a cup with or without intervening lobes or pseudostaminodia; anthers with 2 locules and 1 line of dehiscence. Ovary globose; styles short; stigmas capitate or 2-lobed; ovule 1, suspended from the apex of a slender, elongate funiculus. Utricle slightly compressed, glabrous, indehiscent; seeds globose, brown. (*Cladothrix* (Nutt. ex Moq.) S. Watson, 1880, not Cohn, 1875, Schizomycetes; *Alternanthera* sect. *Cladothrix* Nutt. ex Moq.) TYPE SPECIES: *Alternanthera lanuginosa* (Nutt.) Moq. in DC. = *Tidestromia lanuginosa* (Nutt.) Standley.[6] (Name commemorating Ivar Tidestrom, 1864–1956, Swedish-born American botanist noted for floras of the southwestern United States.)

About six species of southwestern North America, with *Tidestromia lanuginosa* occurring eastward to Cameron and Sabine parishes, Louisiana. The species is evidently native to these localities since it occurs in nearby coastal Texas. It ranges from South Dakota and Kansas to Utah and Nevada, south to Texas, Arizona, northern Mexico and Hispaniola; it is adventive in Missouri and Illinois. The plant occurs in disturbed or severe habitats, such as roadsides, clay banks, limestone-sandy soil, gypsum and gravel washes, and valley silts. Kearney & Peebles noted that it forms conspicuous white mats soon after summer rains on deserts in southern Arizona and that it is adapted for checking the blowing of sandy soils. This species is distinguished from others of the genus by its annual habit and by the absence of pseudostaminodia or the presence of only very short ones. The plants of our area correspond to var. *lanuginosa,* which is characterized by gray-green foliage with stellate trichomes. This variety is distributed throughout the range of the species. Varietas *carnosa* (Steyermark) Cory, with yellowish green, nearly glabrous foliage and very brittle stems, occurs in gypseous saline soils from southern and western Texas southward to Chihuahua, Mexico; it is sometimes recognized as a distinct species, *T. carnosa* (Steyermark) I. M. Johnston.

The genus has not been reviewed throughout its entire range. The other species usually recognized are *Tidestromia gemmata* I. M. Johnston (gypsiferous shales, southwestern Texas and northern Mexico); *T. oblongifolia* (S. Watson) Standley, with subsp. *oblongifolia* (eastern Mojave and Colorado

[6]Only *Alternanthera lanuginosa* was included in sect. *Cladothrix* by Moquin; thus, it is the type of subsequent names based on this section.

deserts eastward into Nevada and Arizona) and subsp. *cryptantha* (S. Watson) Wiggins (western Colorado Desert near the Salton Sea and adjacent slopes); *T. suffruticosa* (Torrey) Standley, with var. *suffruticosa* (rocky soils containing some gypsum, western Texas and southern New Mexico to Coahuila) and var. *coahuilana* I. M. Johnston (somewhat gypseous soil, Coahuila); *T. rhizomatosa* I. M. Johnston (probably a halophytic gypsophile, Coahuila); and *T. tenella* I. M. Johnston (probably gypsophilous, Coahuila).

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6. **Froelichia** Moench, Method. 50. 1794.

Annual [or perennial] herbs [or shrubs] with semi-woody taproots; stems simple to much branched, erect or procumbent, usually densely pubescent. Leaves opposite, short-petiolate [or sessile], most abundant on the lower half of plant, the blades entire, woolly, densely pubescent. Inflorescences interrupted simple or compound spikes mostly on long, erect peduncles; each flower subtended by an adaxial bract persistent on the peduncle and by 2 lateral bracteoles that detach with the fruit. Flowers perfect, sessile. Tepals 5, connate into a 5-lobed perianth tube, the lobes lanceolate, acute, glabrous, and greenish white or pinkish and the tube lanate, becoming indurated in fruit and bearing crests or tubercles. Stamens 5; filaments connate into a tube with the 5 anthers sessile between the 5 lobes of the staminal tube; anthers with 2 locules and 1 line of dehiscence. Style 1, somewhat elongate [or nearly absent], shorter than the staminal tube; stigma sessile, capitate, irregularly lobed [or penicillate]; ovary ovoid; ovule solitary, pendulous from the tip of a long funiculus, the micropyle superior. Fruit a small, ovoid, membranaceous, indehiscent utricle enclosed by the indurated perianth tube; mature perianth tube with 2 longitudinal rows of spines or irregularly toothed wings and 3 basal tubercles; seed obovoid or lenticular, smooth, inverted;

embryo annular, surrounding the central, mealy perisperm, the radicle superior; usually germinating while enclosed by the perianth tube. (*Oplotheca* Nutt., *Hoplotheca* Sprengel, *Ninanga* Raf., and *Everior* Raf.) TYPE SPECIES: *F. lanata* Moench = *F. interrupta* (L.) Moq. in DC. (Name honoring Joseph Aloys Froelich, 1766–1841, German physician and botanist who published on *Sonchus, Hieracium,* and *Gentiana.*) — COTTONWEED, SNAKEWEED.

Perhaps 12 species of the eastern, central, and southwestern United States; Mexico; most of the Greater Antilles; the Galapagos Islands; and South America from Colombia to Paraguay, Chile, Brazil, and Argentina. Six species occur in North America, two in our area. The greatest diversity appears to be in southwestern North America and in Brazil. A modern review of the genus is needed (the last was by Schinz, 1933), particularly in terms of the relationships of the species of South America and those of southwestern North America.

Froelichia gracilis (Hooker) Moq. is distinguished from other species of the genus by its asymmetrically conical fruiting perianths less than 4 mm. long with crests of lateral rows of distinct spines, tannish seeds, leaves mostly 5–10 mm. wide, and stems much branched from the base. This species occurs mostly in sandy soil from Iowa to Colorado, southward to Arkansas, Texas, New Mexico, and Mexico; it is widely adventive eastward to Wisconsin, Illinois, Indiana, New York, New Jersey, Maryland, Virginia, North Carolina, South Carolina, Georgia, Alabama, and Mississippi. In areas where it is introduced, it is usually found along railroad tracks in cindery soil.

Froelichia floridana (Nutt.) Moq. (leaves mostly 10–30 mm. wide; mature fruiting perianths over 5 mm. long, flask shaped, the crests deeply dentate with irregular margins; seeds dark red-brown; stems branching profusely only in the upper nodes) occurs from Delaware, New Jersey, Indiana, Minnesota, South Dakota, and Colorado to Florida, Mississippi, and Texas. Two distinct varieties are recognized. Varietas *floridana* has taper-tipped elliptic-lanceolate leaves that are canescent to subscabrous above, puberulent or tomentulose branches with short trichomes, and peduncles with trichomes less than 0.5 mm. long. This variety occurs on the Coastal Plain from Florida north to Delaware and New Jersey, and west to Mississippi and Texas. Varietas *campestris* (Small) Fernald (*F. campestris* Small) has oblanceolate or subspathulate, obtuse-tipped leaves that are canescent or silky on the upper surface, sericeous-tomentose branches, and lanate peduncles with the trichomes commonly 2 mm. long; it ranges from Indiana, Wisconsin, Minnesota, and South Dakota, southward to Illinois, Missouri, Kansas, Arkansas, Oklahoma, Texas, and Colorado. Both varieties are usually found in sandy soil.

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7. **Alternanthera** Forsskål, Fl. Aegypt. Arab. 28. 1775.

Annual or perennial herbs [shrubs or rarely small trees]; stems prostrate, decumbent, ascending, erect, or floating, often pubescent with simple, dentate, or barbed trichomes; taproot often present and robust. Leaves opposite, entire, sessile or petiolate, the blades narrow to broad. Inflorescences axillary or terminal, sessile or pedunculate, globose or cylindrical, usually whitish or silvery headlike spikes; bract and bracteoles scarious, the latter keeled. Flowers perfect, or imperfect by malformation. Perianth often dorsally compressed, of 5 free, equal or unequal, glabrous or variously pubescent tepals, 2 more concave than the rest. Stamens usually 5, sometimes anthers missing from some filaments; filaments connate basally into a tube or short cup; pseudostaminodia 5, ligulate, subulate, or reduced to small teeth, or rarely absent, entire to laciniate, alternating with antheriferous filaments on the androecial tube; anthers with 2 locules and 1 line of dehiscence. Ovary globose or ovoid, compressed or not; style usually short; stigma capitate, seldom bilobed, the papillae often elongate; ovule 1, suspended from the tip of an elongate, basal funiculus, the micropyle superior; spurious carpels sometimes produced on androecial tube. Utricle compressed, ovoid or obovoid, sometimes corky, falling off with the perianth and with or without the bracteoles, the margin often narrowly winged, seed lenticular, and seed coat semipellucid or coriaceous, smooth; embryo annular, surrounding the mealy perisperm, the cotyledons narrow, the radicle superior. (*Achyranthes* sensu Standley, Jour. Wash. Acad. Sci. **5:** 72. 1915, not L., 1753; *Telanthera* R. Br.) TYPE SPECIES: *Gomphrena sessilis* L. = *A. sessilis* (L.) DC.; see R. Melville, Kew Bull. **13:** 171. 1958. (Name from Latin *alternans*, alternating, and *anthera*, anther, referring to the alternation of pseudostaminodia with antheriferous filaments). — CHAFF FLOWER.

Approximately 80 species according to Mears, but some estimates as high as 200. The vast majority of species occur in the American tropics and subtropics, with a few in Africa, Asia, and Australia; 16 species or subspecies, 11 of them endemic, occur in the Galapagos Islands. Several species are

aggressive weeds that have become naturalized in many parts of the world. Since Moquin-Tandon's treatment of the family for De Candolle's *Prodromus* (1849), the genus has been revised only regionally. As recent investigators have examined species over broader geographic areas, there have been numerous name changes; there will doubtless be more as revisionary work continues. The genus has been divided into several sections, but because of the present lack of knowledge of many species, subdivisions are not recognized in most floristic works. Seven species (three of them introduced) occur in the southeastern United States. See the discussion under *Achyranthes* concerning Standley's unfortunate application of that name to this genus.

Two species in our area have long-pedunculate axillary and terminal inflorescences. *Alternanthera philoxeroides* (Mart.) Griseb. (*Achyranthes philoxeroides* (Mart.) Standley), alligator weed, $2n = 28, 100$, a native of South America, has become naturalized in ponds, ditches, streams, and bayous on the Coastal Plain from North Carolina to Florida, west to Louisiana and southeastern Texas; it occurs also in much of South America and is widely scattered, but infrequent, in Central America and the West Indies, and in parts of the Old World. This vigorously growing plant, along with water hyacinth (*Eichhornia crassipes*, Pontederiaceae), clogs waterways in the southeastern United States. It is an aquatic to semiterrestrial perennial herb, often forming mats, with sessile flowers and linear to lanceolate-ovate leaf blades; the stems (except for the upper internodes), tepals, and leaves are nearly glabrous. *Alternanthera flavescens* HBK. (*A. ramosissima* sensu auct.), with shortly pedicellate flowers, ovate or elliptic leaves, and pubescent stems and tepals, occurs in coastal hammocks and thickets and on sand bars in southern Florida; it also occurs in Mexico, the West Indies, and South America.

The other species of *Alternanthera* in our area have inflorescences that are essentially sessile (the peduncles less than 1 cm. long) in the axils of leaves. Three have elongate androecial tubes with the pseudostaminodia laciniate and equaling or exceeding the filaments. *Alternanthera maritima* (Mart.) St. Hil. (*Achyranthes maritima* (Mart.) Standley, *Telanthera maritima* (Mart.) Moq.), with procumbent or prostrate stems, fleshy ovoid leaves, and glabrous, rigid, striate tepals, occurs along sandy beaches and in hammocks in southern peninsular Florida; it also is found in Bermuda, the West Indies, Brazil, and West Africa. *Alternanthera tenella* Colla (*A. ficoidea* sensu many authors, not (L.) Beauv.; see Veldkamp, Mears), with erect stems, nonfleshy, green leaves, and sparsely pilose, marginally chartaceous tepals, may be locally naturalized in our area, but I have seen no documenting specimens. This variable species of Mexico, Central America, South America, and the West Indies is often divided into several varieties or segregate species. A related species, *A. Bettzichiana* (Regel) Voss (*Achyranthes Bettzichiana* (Regel) Standley; including *Al. amoena* (Lem.) Voss), parrotleaf, calico plant, a widely cultivated, variable plant, often with brightly colored foliage, is native to Brazil but has escaped in many parts of the world, including southern Florida. (See Mears regarding the spelling *Bettzichiana* vs. *Bettzickiana*.)

The three other species of *Alternanthera* in our area have short androecial tubes and pseudostaminodia that are entire or dentate and shorter than the

staminal filaments. *Alternanthera paronychioides* St. Hil. (*A. polygonoides* (L.) R. Br.; *Achyranthes polygonoides* (L.) Lam., *Gomphrena polygonoides* L., *pro parte*, see Pedersen, 1967), $2n = 34, 96$, distinguished by its ± equal tepals 3–5 mm. long that lack rigid, spinose tips and by leaves that are

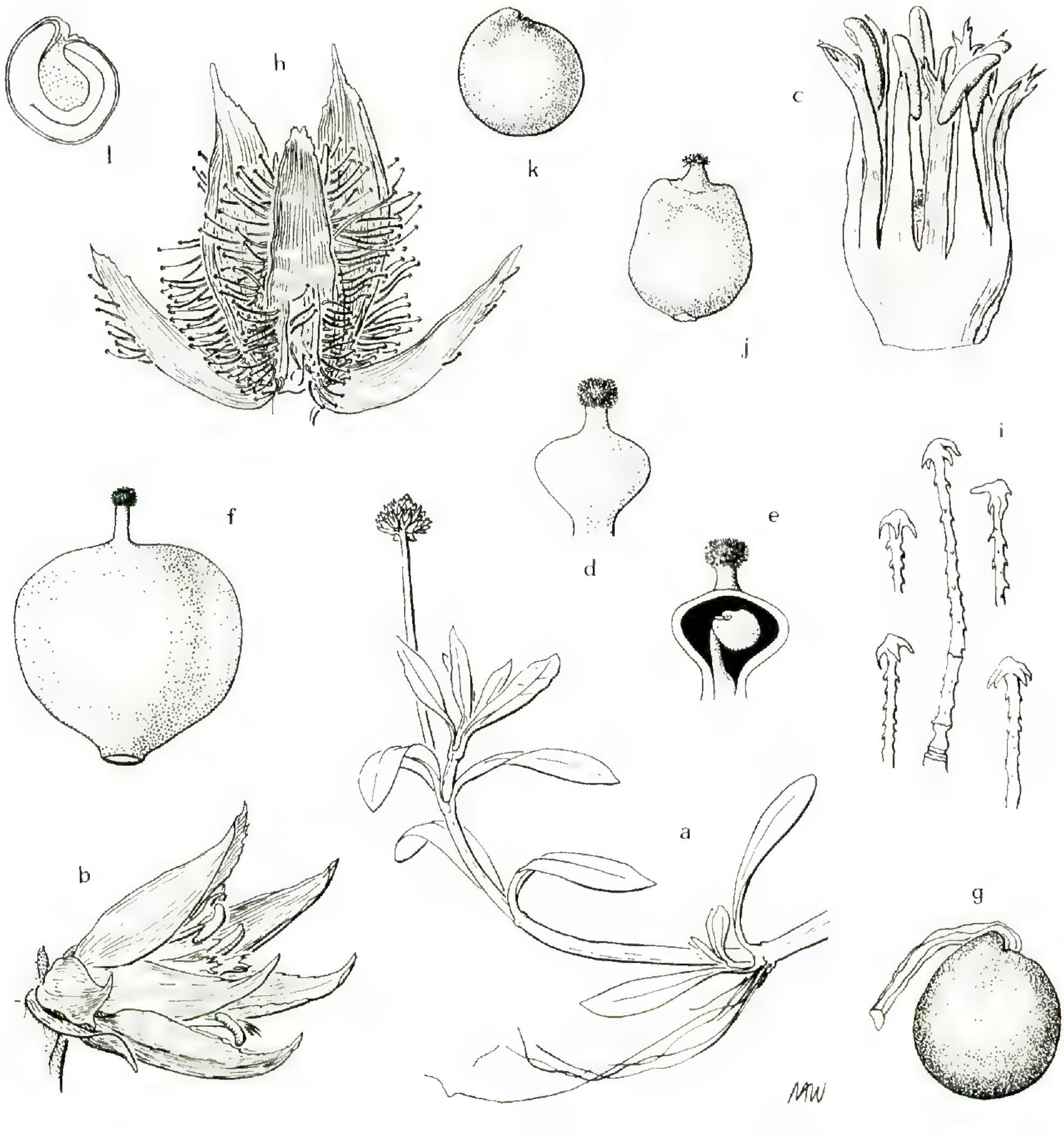

FIGURE 3. **Alternanthera.** a–g, *A. philoxeroides:* a, tip of stem with inflorescence, × ½; b, lateral view of flower showing subtending bract and one of two lateral bracteoles, × 5; c, androecium with five fertile stamens alternating with five pseudostaminodia (stigma barely visible within), × 10; d, gynoecium, × 10; e, same, with part of ovary wall removed to show ovule on elongate funiculus, × 10; f, fruit (from an Uruguayan specimen), × 8; g, seed with persistent funiculus (also from Uruguay), × 8. h–l, *A. caracasana:* h, flower from above to show two lateral bracteoles and heteromorphic tepals, × 10; i, glochidiate trichomes from tepals, × 48; j, fruit, × 10; k, seed, funiculus removed, × 10; l, diagrammatic vertical section of seed, perisperm stippled, × 10.

about twice as long as broad, occurs near salt water from North Carolina to southernmost Florida, west to Alabama, Louisiana, and Texas; it is also found in Mexico, Central America, South America, the West Indies, Africa, and India, and on some Pacific islands. *Alternanthera pungens* HBK. (*A. repens* (L.) Link, not Gmelin nor American authors, see Melville; *Achyranthes leiantha* (Seub.) Standley), $2n = 64$, with spinose-tipped, sparsely villous tepals 4–7 mm. long, leaf blades as long as broad (up to 2 × 2 cm.), and dentate pseudostaminodia, is a variable South American species that is adventive in Florida, Alabama, and Texas; it is also found in Cuba, Jamaica, Africa, India, Thailand, Australia, and Hawaii. *Alternanthera caracasana* HBK. (*Achyranthes repens* sensu American authors, not L.; *Al. peploides* (Willd. ex R. & S.) Urban), with spinose-tipped, densely villous tepals 3–5 mm. long, leaf blades longer than broad (up to 1.5 × 1 cm.), and entire pseudostaminodia, ranges from South Carolina to Florida, west to Texas and California; it also occurs in South America, Africa, and the Canary Islands.

Alternanthera philoxeroides was first reported in the southeastern United States in Florida in 1894. Since then it has spread northward along the Coastal Plain to North Carolina and Virginia and westward to Tennessee, Arkansas, and Texas; it has also become established locally in southern California. It has been estimated that by 1970 the plant had infested between 27,000 and 65,700 hectares (66,770 to 162,000 acres) of water in North and South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas. Reproduction is by fragments of plants (viable seeds are evidently not produced in the United States). The species occurs in moist soil along bodies of water, rooted in shallow water, or in floating mats in deeper water, in which the interwoven stems may extend 1 m. or more down into the water and up to 100 m. over the surface. Native vegetation cannot compete with the weed, so nearly pure stands are formed, unlike the almost inconspicuous occurrence of the plant in undisturbed habitats in southern South America. Chemical herbicides are not consistently effective in controlling it, and there are no serious natural insect pests in the United States. Since 1964, three South American insects have been released as biological control organisms in the United States: *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae), alligatorweed flea beetle; *Amynothrips andersoni* O'Neill (Thysanoptera: Phlaeothripidae), alligatorweed thrips; and *Vogtia malloi* Pastrana (Lepidoptera: Pyralidae: Phycitinae), alligatorweed stem borer. "These insects are now providing substantial control of alligatorweed over the entire range where the weed occurred as an aquatic plant problem. It is our contention that alligatorweed will cease to be an important aquatic weed and only rarely will be found in pure stands in any significant proportions in the United States of America" (Spencer & Coulson).

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8. **Gomphrena** Linnaeus, Sp. Pl. **1:** 224. 1753; Gen. Pl. ed. 5. 105. 1754.

Annual or perennial herbs [caespitose subshrubs, or lianas], the stems usually pubescent and much branched from near base and wide spreading, ascending, decumbent, prostrate, or erect, sometimes rooting at the nodes; nodes often swollen; [roots often tuberous or a deep taprootlike caudex]. Leaves opposite [alternate, fascicled, or mostly basal], shortly petiolate or sessile [often partly clasping at base], the blades entire, ovoid to obovate [linear, lanceolate, or circular], usually pubescent at least below. Inflorescences of terminal and/or axillary, many-flowered, sessile [to long pedunculate], subglobose [discoid or cylindrical] heads [or short to elongated spikes], often subtended by an involucre of sessile leaves, the heads solitary [or forming an interrupted spike or arranged in open panicles]; bracts and bracteoles thin [to scarious or subcoriaceous], white or colored [often brilliantly], the bracts persistent, glabrous [or sparsely pubescent], strongly concave or folded, the bracteoles glabrous, ± deciduous, usually longer than the bracts and equaling [or exceeding] the tepals, the abaxial surface often with a denticulate, laciniate [serrate, or entire] crest. Flowers perfect. Tepals

white [or colored], connate below [or free], strongly concave, scarious, abaxially densely long-pubescent [rarely glabrous], entire [or serrate]. Androecium of 5 monadelphous stamens, the tube included [or exserted], sometimes slightly adaxially curved, white to ± colored, containing nectar; each free filament segment mostly 3-parted at the apex with 2 variously shaped lateral lobes and a central, slender, often very short antheriferous lobe; anthers introrse, dorsifixed, oval to linear, with 2 locules and 1 line of dehiscence; pseudostaminodia absent. Style 1, ± elongate [to very short or absent], usually included within staminal tube; stigmas 2 or rarely 3 [or 1 and then bilobed], the branches mostly erect, slender and subulate or filiform; ovary subglobose [ovoid, turbinate, or cylindrical], slightly compressed; ovule 1, suspended from the apex of an elongated, basally attached funiculus, the micropyle superior; base of ovary surrounded by a prominent disc. Fruit an ovoid or oblong, somewhat compressed, indehiscent utricle usually included within the persistent tepals and staminal tube, the fruit wall very thin, membranaceous; seed lenticular, smooth, lustrous, reddish brown [brown, or yellowish], the seed coat coriaceous; embryo annular around the mealy perisperm, the cotyledons obovate or narrow, the radicle slender, superior. LECTOTYPE SPECIES: *G. globosa* L.; see P. C. Standley, N. Am. Fl. **21:** 147. 1917, and A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 137. 1929. (Name perhaps a modification of the Latin name, *gromphaena*, used by Plinius for a kind of amaranth; from Greek *gomphros*, "*clavis ligni*," according to Linnaeus.) — GLOBE-AMARANTH.

An estimated 100 species, originally restricted to the tropics, subtropics, and warm-temperate regions of the New World, except for approximately 18 species essentially of Australia. The last complete taxonomic treatment of the American taxa (Holzhammer, 1955) recognized 95 species in five sections; Mears (1980) has reviewed those originally described by Linnaeus as species of *Gomphrena*.

In our area, apparently indigenous plants of *Gomphrena* occur along roadsides, ditches, beaches, and in waste areas in peninsular Florida. These have been recognized as two species, *G. decumbens* Jacq., $2n = 18, 26$, and *G. dispersa* Standley, considered by Holzhammer to be closely related species of sect. GOMPHRENA. Mears, however, includes both of these within *G. serrata* L., "the most common and most widely distributed noncultivated species of *Gomphrena*." The general distribution of *G. serrata* is in Florida, southern Texas, the Greater Antilles, Mexico, Central America, and (apparently disjunctly) in Bolivia and Paraguay. *Gomphrena globosa* L., globe-amaranth, $2n = 44$, is very commonly cultivated in our area and may persist after or escape from cultivation; it was collected in St. Landry Parish, Louisiana, by Correll and Correll (*9468*, GH).

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9. **Iresine** P. Browne, Civil Nat. Hist. Jamaica, 385. 1756, nomen conserv.

Annual or perennial herbs [subshrubs, shrubs, or small trees] from taproots, horizontal rhizomes [or branching rootstocks], the stems ± pubescent or glabrous, unbranched to much branched, erect to prostrate, often trailing, the nodes somewhat swollen. Leaves opposite, petiolate, the blades thin [to somewhat fleshy], entire or serrulate. Inflorescences of small, crowded spikes [or heads] arranged in many-flowered, mostly open panicles terminating stems and in axils of upper leaves; each flower subtended by a bract and 2 bracteoles, all membranaceous, shining, silvery white [stramineous or fuscous], glabrous to slightly [or densely] pubescent. Flowers small or minute,

usually imperfect and the plants monoecious, dioecious, or polygamous. Perianth of 5 basally connate or free, subequal, membranaceous, silvery white to stramineous, 1- to 3-nerved, abaxially glabrous or pubescent tepals, those of the carpellate flowers subtended by a ring of trichomes that elongate greatly in fruit. Androecium mostly of 5 stamens (these greatly reduced or lacking in carpellate flowers), the filaments basally connate, the anthers introrse, dorsifixed, with 2 locules and 1 line of dehiscence; pseudostaminodia absent or short. Style 1, very short or absent; stigmas 2 or 3, usually elongate, stout to filiform; ovary compressed in carpellate flowers, absent or rudimentary in staminate flowers; ovule 1, suspended from the top of the ovary by an elongate funiculus, the micropyle superior; all flowers with a prominent, 5-lobed disc. Fruit a very small, indehiscent, membranaceous, silvery white, ± globose utricle subtended by copious very long trichomes and at maturity falling away from the bracts; seed smooth, lenticular, inverted, reddish to red-brown; embryo annular around the mealy perisperm; cotyledons narrow, the radicle superior. TYPE SPECIES: *Celosia paniculata* L. = *I. diffusa* Humb. & Bonpl. ex Willd. (Name evidently derived from Greek *eiresione,* a wreath or staff wrapped with fillets of wool, perhaps for the ring of long trichomes that subtend the tepals of many species.) — BLOODLEAF.

Perhaps 70 species mostly of the tropics and subtropics of the New World; also in Australia and the Galapagos Islands. Two species are indigenous to the southeastern United States.

Iresine diffusa Humb. & Bonpl. ex Willd.[7] (*I. paniculata* (L.) Kuntze not Poiret, *I. Celosia* L., *I. celosioides* L., *I. canescens* Humb. & Bonpl. ex Willd.), commonly called "Juba's bush," a dioecious, annual herb (sometimes persisting for several years from a vertical rootstock) with erect, spreading, or clambering, much-branched stems and 3-nerved tepals that exceed the utricle, occurs in hammocks, marshes, and other habitats, mostly along the coast, supposedly from North Carolina southward to Florida and west to Texas; it also occurs in the West Indies, Mexico, Central America, and much of South America. Although reported from North Carolina by Reed (1969), Standley (1917), and Small (Man. S. E. Fl.), it was not included by Radford, Ahles, & Bell in their *Manual of the Vascular Flora of the Carolinas.*

Iresine rhizomatosa Standley (*I. paniculata* sensu Uline & Bray, not L.; *I. Celosia,* in part, of American authors, not L.; *I. celosioides* Michaux, not L.), a perennial, dioecious, stoloniferous herb with the erect stems largely unbranched below the inflorescence and with 1-nerved tepals that are shorter than the utricles, is mostly found in sandy alluvial soils of low woods and in depressions and sand dunes and along rivers from Maryland, southeastern Virginia, coastal North and South Carolina, Georgia, Florida, and Alabama, westward to Tennessee, southern Illinois, Missouri, Arkansas, southern

[7]Mears and Gillis adopt the name *I. canescens* Humb. & Bonpl. ex Willd. for this species; however, Shinner's usage of *I. diffusa,* which dates from the same time as *I. canescens,* must be followed in accordance with Article 57 of the International Code of Botanical Nomenclature.

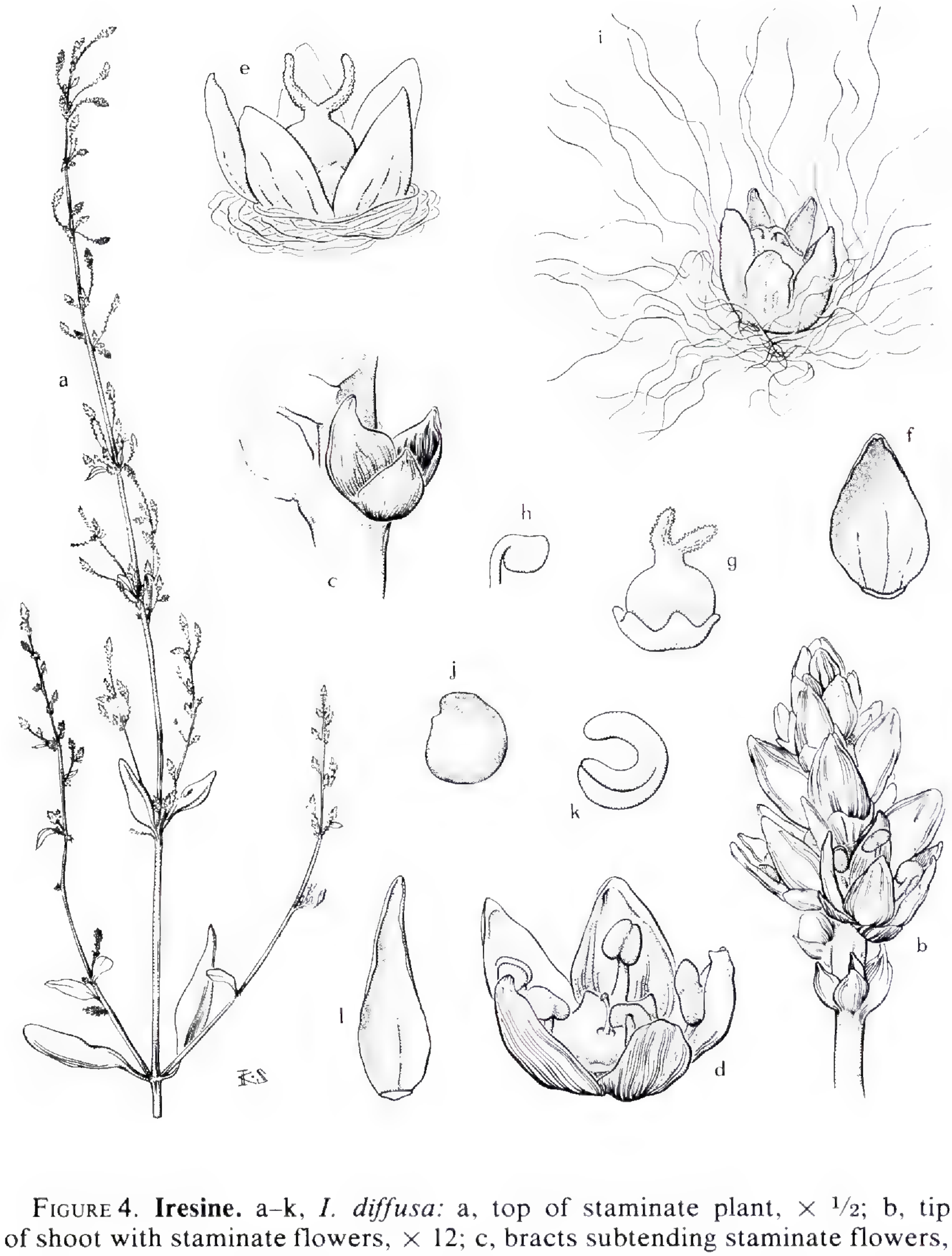

FIGURE 4. **Iresine.** a–k, *I. diffusa:* a, top of staminate plant, × 1/2; b, tip of shoot with staminate flowers, × 12; c, bracts subtending staminate flowers, flowers removed, × 25; d, staminate flower, stamens opposite tepals—note rudimentary gynoecium in center of flower, × 25; e, carpellate flower, surrounded at base by swirl of subtending trichomes, × 25; f, tepal of carpellate flower—note three veins, × 25; g, gynoecium with disc at base, × 25; h, ovule and funiculus, × 25; i, mature fruit with persistent tepals and unfurled subtending trichomes, × 12; j, seed, × 25; k, embryo, oriented as in "j," × 25. l, *I. rhizomatosa:* tepal of carpellate flower showing single vein, × 25.

Louisiana, Oklahoma, and southeastern Texas.

Standley (1917, family references) attributed *Iresine flavescens* Humb. & Bonpl. ex Willd. to southern Florida, but I have seen no specimens to document this; Mears & Gillis consider the species to be endemic to the West Indies.

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10. **Philoxerus** R. Brown, Prodr. Fl. Novae Holland. 416. 1810.

Procumbent or creeping, much-branched, somewhat succulent or fleshy, perennial or annual herbs [or low shrubs], the branches often ascending. Leaves opposite, sessile, thick and fleshy [or not], linear to narrowly obovate [or subulate], amplexicaulous, entire, glabrous except for tufts of trichomes in the axils. Inflorescences headlike or cylindrical [to elongate], many-flowered, pedunculate spikes solitary and terminal on branches; bracts and bracteoles chartaceous, 1-nerved, the bract expanded, the 2 bracteoles keeled. Flowers perfect, silvery white or pink, the pedicels very short, thick, white-lanate. Perianth of 5 unequal, dorsiventrally compressed, chartaceous, basally thickened and connate tepals, the outer 3 glabrous, the inner 2 abaxially lanate at the base. Stamens 5, filaments included, connate below into a short cup; anthers much shorter than the filaments, with 2 locules and 1 line of dehiscence; pseudostaminodia absent. Ovary dorsiventrally compressed, broadly ovoid; style very short; stigmatic branches 2 or 3, subulate; ovule solitary, pendulous from the tip of an elongate funiculus. Utricle somewhat compressed, broadly ovoid, coriaceous, thin, indehiscent or tearing irregularly; seed orbicular or lenticular, smooth, the seed coat coriaceous, lustrous brown, inverted; embryo annular around the mealy perisperm, the cotyledons narrow, the radicle superior. LECTOTYPE SPECIES: *P. conicus* R. Br.; see P. C. Standley, N. Am. Fl. **21:** 168. 1917. (Name evidently derived from Greek *philos,* loving, and *xeros,* dry, in reference to the habitat of species of the genus.)

As presently recognized, approximately 10 species, mostly littoral, in the tropics and subtropics of the Atlantic and Caribbean regions of the Americas, and western Africa, northern Australia, the Ryukyu Islands, and the Galapagos Islands. However, Mears (1980) says that the three Australian species originally placed in *Philoxerus* by Brown are now generally placed in *Gomphrena,* and

that it is necessary to revive the name *Caraxeron* Vaill. ex Raf. for the species now known as *Philoxerus vermicularis* (L.) J. E. Sm. and its relatives. Mears[8] is preparing a paper about this change, and the name *Caraxeron vermicularis* (L.) Raf. was used for this taxon in Kartez & Kartez (family references).

Philoxerus vermicularis (L.) J. E. Sm.,[9] silverhead, saltweed, samphire, a much-branched, perennial or sometimes annual herb with mostly prostrate stems, ascending branches, and globose to cylindrical, compact inflorescences that are white or pinkish when alive, drying silvery white, occurs in saline soils and sand of beaches, dunes, and sand bars along both eastern and western coasts of Florida, to Louisiana and Texas; it also ranges southward through Mexico to Panama, Colombia, and Brazil, in the West Indies, and on the western coast of tropical Africa.

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172 NATURAL RESOURCES BUILDING
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[8]Note added in proof: Mears (pers. comm.) has had two papers accepted for publication in *Taxon*, one treating the Australian species as *Philoxerus*, and the other placing the American species in *Blutaparon* Raf. instead of *Caraxeron* since Rafinesque included both the Australian and the American species in *Caraxeron*.

[9]The transfer of *Gomphrena vermicularis* L. to *Philoxerus* is usually attributed to R. Brown, Prodr. 416. 1810, but Brown merely indicated that *G. vermicularis* seemed to belong to *Philoxerus* and did not make the formal transfer. The first transfer appears to be by J. E. Smith in Rees, Cyclop. **27** [alph. ord.]. 1814, as *P. vermiculatus*, sphalm.

A MONOGRAPH OF LYONIA (ERICACEAE)*

WALTER S. JUDD

Lyonia Nutt. sect. LYONIA

Andromeda sect. *Hemiclis* Raf. New Fl. N. Am. pt. 4. 107. 1836 [1838]. LECTOTYPE SPECIES: *Lyonia ferruginea* (Walter) Nutt.

Lyonia Nutt. subg. *Eulyonia* K. Koch, Dendr. **2:** 119. 1872, *nomen illegit.* *Andromeda* L. subg. *Lyonia* (Nutt.) Gray, Synopt. Fl. N. Am. **2**(1): 32. 1878. *Xolisma* Raf. sect. *Lyonia* (Nutt.) Rehder, Jour. Arnold Arb. **5:** 54. 1924. TYPE SPECIES: *Lyonia ferruginea* (Walter) Nutt.

Evergreen shrubs to medium-sized trees, sometimes from an underground woody burl but usually not spreading vegetatively by horizontal underground rhizomes, the branches with homogeneous pith. Indumentum of unicellular hairs and multicellular, biseriate-stalked, peltate scales. Buds with 2 rather small, imbricate scales. Leaves entire, obscurely and irregularly toothed or notched, to clearly toothed, with lignified epidermis and often lignified hypodermis. Flowers 4- to 7-merous, in dense axillary fascicles to (less commonly) short racemes; calyx lobes very slightly imbricate in bud; corolla cylindrical, long- to short-urceolate, or campanulate; filaments merely roughened (lacking unicellular hairs), unappendaged or with pair of small to well-developed spurs near apex; placentae positioned subapically on columella. Capsules with pale, much-thickened sutures separating as unit from valves in dehiscence; seeds linear to spindle shaped, tailed.

DISTRIBUTION. North America, Coastal Plain from Florida to South Carolina; montane areas of eastern and southern Mexico; Greater Antilles (including St. Thomas).

NUMBER OF SPECIES (taxa). 27 (34).

COMMON NAMES. Most species of this group lack specific common names; many Cuban species are called "clavellina," a name applied to several different shrubs with showy flowers that grow along margins of rivers or arroyos, or in moist areas (Roig, 1953, 1965). In the Dominican Republic many lyonias are known as "palo de reina" (Liogier, 1974).

The indumentum, thickness, and various anatomic characters (for example, presence of lacunae, epidermal lignification, and presence of hypodermis) of the leaf blades are especially important in this section. The variation in these features is shown in FIGURES 31–33.

*Continued from Volume 62, page 209.
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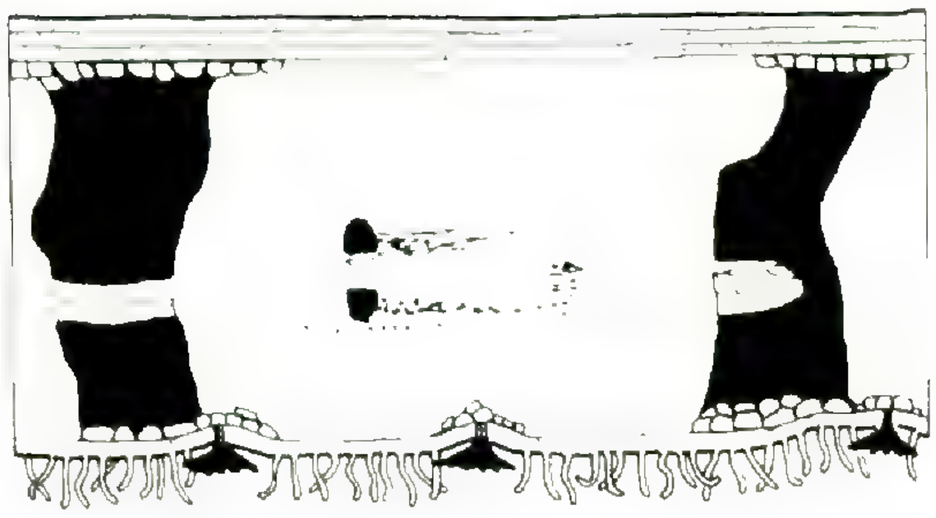
Journal of the Arnold Arboretum **62:** 315–436. July, 1981.



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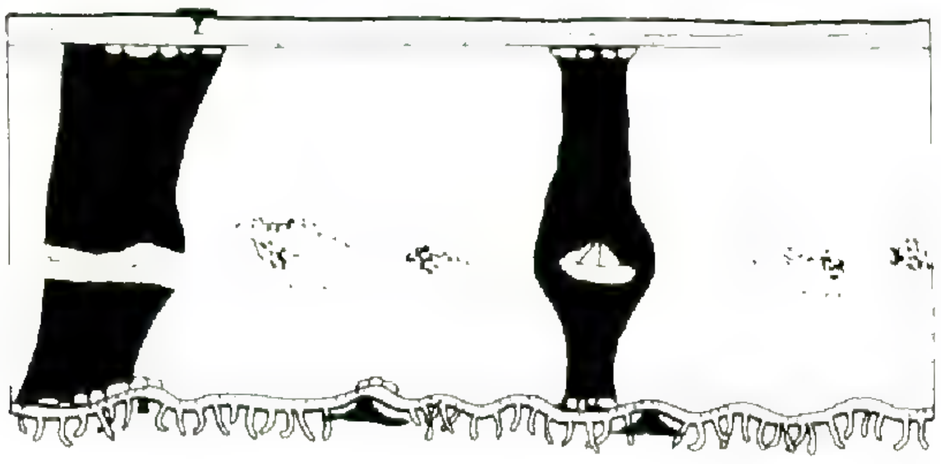

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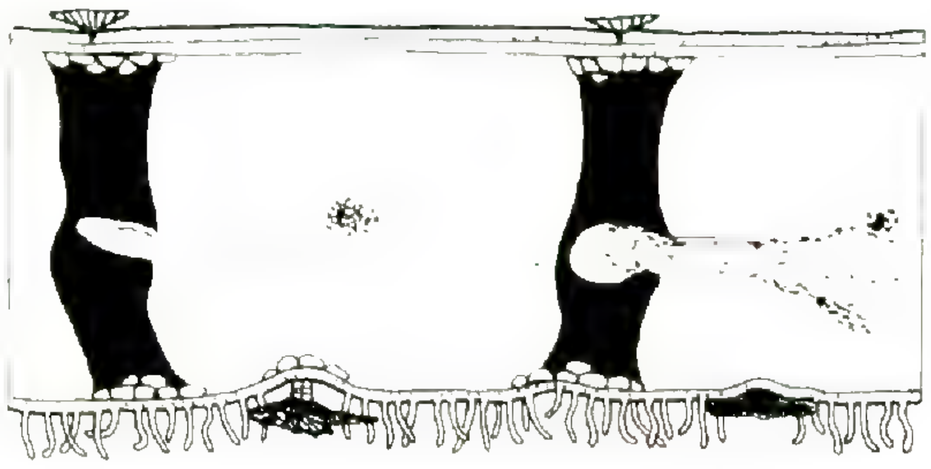

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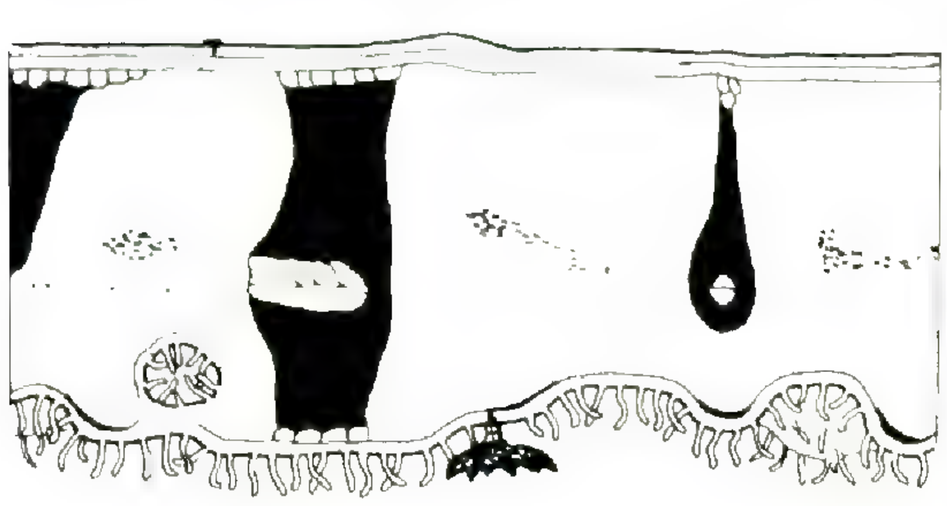

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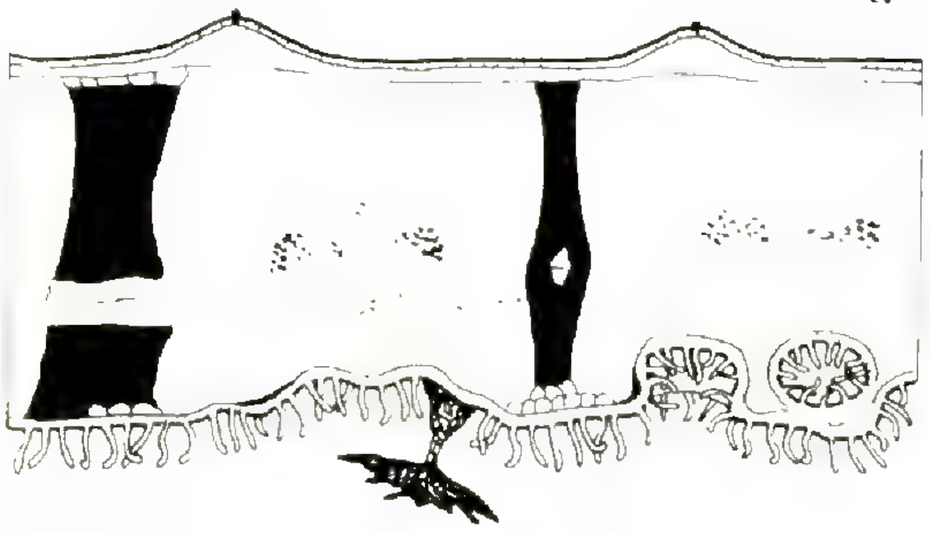

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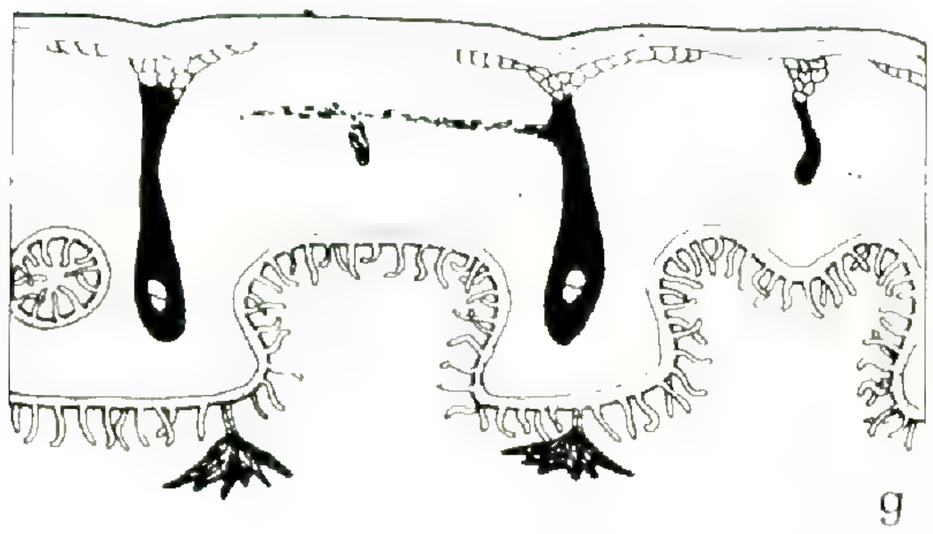

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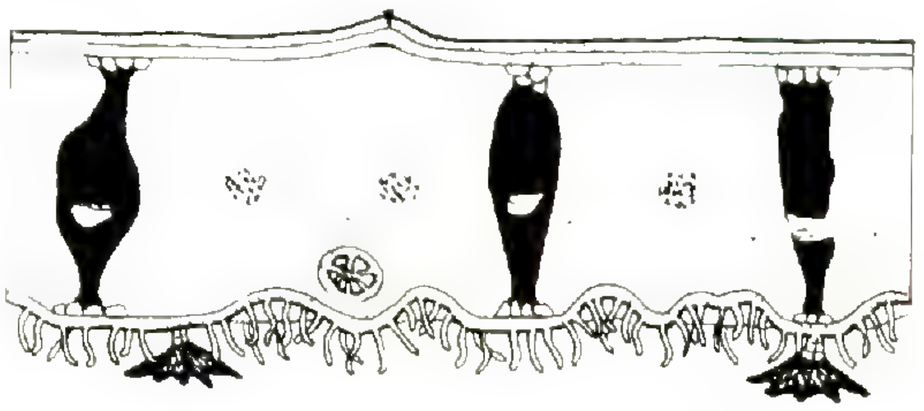

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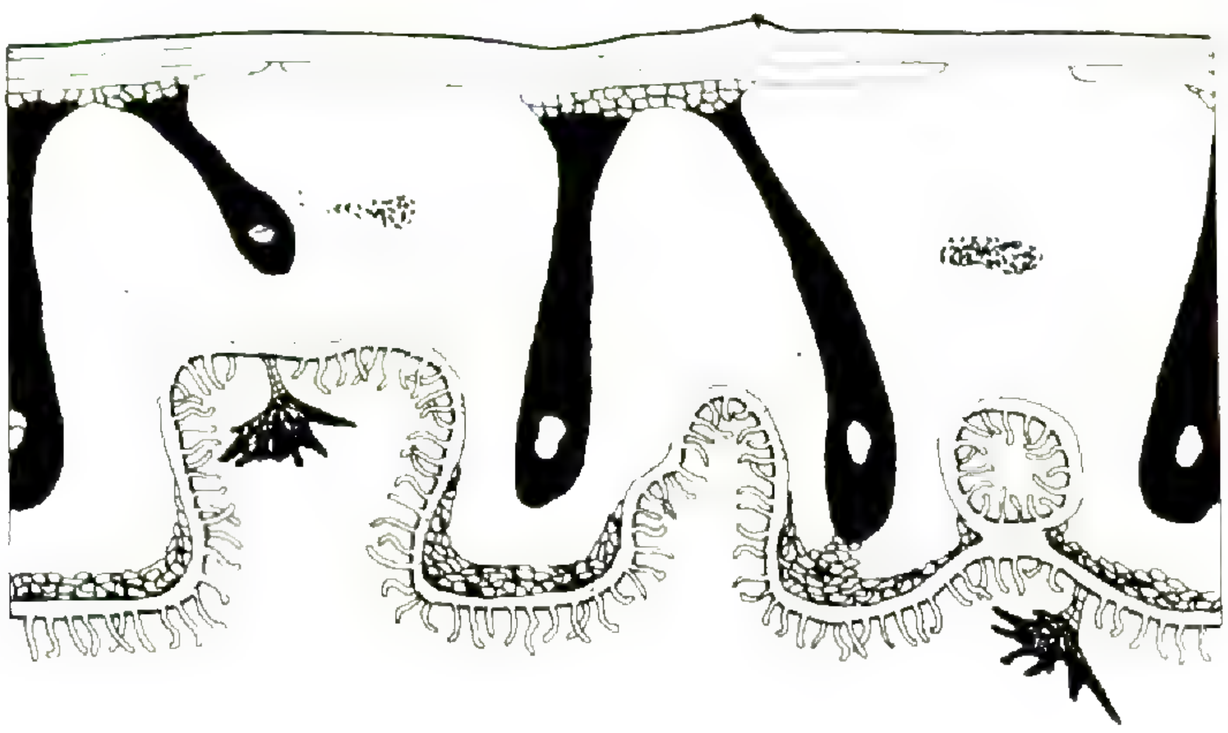

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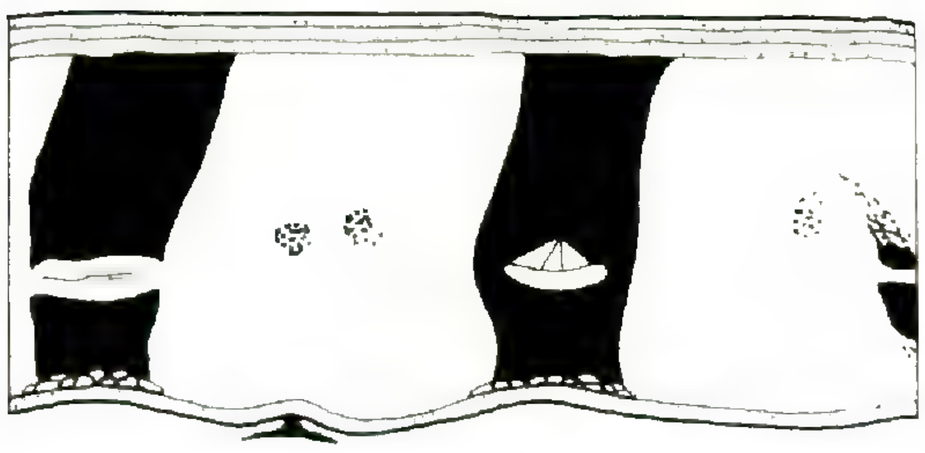
9. **Lyonia heptamera** Urban, Symb. Antill. **1:** 376. 1899.

Xolisma heptamera (Urban) Small, N. Am. Fl. **29**(1)**:** 67. 1914. TYPE: Dominican Republic, Pico del Valle, 2630 m. alt., 30 May 1887, *Eggers 2199* (holotype, B (destroyed); isotypes, K!, L!, M!, P!).

Lyonia dictyoneura Urban, Symb. Antill. **7:** 533. 1913. *Xolisma dictyoneura* (Urban) Small, N. Am. Fl. **29**(1)**:** 67. 1914. TYPE: Dominican Republic, prov. Azua, summit of Culo de Maco, 2225 m. alt., August 1912, *Fuertes 1969* (holotype, B (destroyed); fragment of holotype, NY!).

Low evergreen shrub, usually not over ca. 2 meters tall, generally from an underground woody burl, with gray, longitudinally furrowed bark. Twigs slightly angled, usually stout, sparsely to moderately lepidote, otherwise glabrous. Buds ovoid, 2–4 by 2–3 mm. Leaf blades ovate, 2–6(–9) by 1.7–5(–6.7) cm., ± flat, thick-coriaceous, ca. 0.4–0.7 mm. thick; apex slightly acuminate or acute, to truncate or rounded; base cordate to less commonly rounded (to cuneate in immature plants); margin revolute or plane, distal portion irregularly undulate to obscurely toothed, proximal portion undulate to entire; venation brochidodromous, 3° veins reticulate to percurrent; adaxial surface often roughened by thickened scale bases, especially near margin or toward apex, lepidote but scales usually quickly deciduous, glabrous on midvein, the veins usually slightly depressed, ± obscure above 4°; abaxial surface moderately to densely lepidote, otherwise densely pubescent, all veins prominently raised and forming conspicuous network; scales rust colored, deciduous to persistent, ca. 0.07–0.22 mm. in diameter, erose to nearly entire; petiole 4–10 mm. long, lepidote, otherwise glabrous. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate to shortly racemose, 4- to 13-flowered. Pedicels clearly articulated with calyx, stout, 5–20 mm. long, lepidote, otherwise pubescent; bracteoles opposite to subopposite, basal or nearly so, narrowly triangular, 2–6 mm. long; bracts 4–9 mm. long, usually caducous. Flowers (5- or) 6- or 7- (or 8-)merous; calyx lobes triangular, with acuminate apices, (2–)2.5–6 by 1.5–5 mm., the adaxial side slightly pubescent, especially at margins and near apex, the abaxial side densely lepidote, otherwise moderately to densely pubescent; corolla carnose, urceolate, 8–13 by 8–13 mm., white to pink tinged, especially near mouth, abaxially densely to moderately lepidote; filaments roughened, 4.5–7 mm. long, unappendaged or with spurs to ca. 0.6 mm. long near junction with anthers, anthers 2–4 mm. long; ovary lepidote, otherwise pubescent, placentae subapical to nearly central. Capsule subglobose to short-ovoid, 4–7 by 7–10.5 mm., moderately to densely lepidote, otherwise sparsely to densely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.5–2 mm. long. (FIGURES 34, 35).

FIGURE 31. Cross sections of leaf blades of various species of *Lyonia* sect. LYONIA, × 50: a, *L. alpina;* b, *L. alainii;* c, *L. truncata* var. *montecristina;* d, *L. truncata* var. *truncata;* e, *L. tinensis;* f, *L. urbaniana;* g, *L. buchii;* h, *L. microcarpa;* i, *L. heptamera.*



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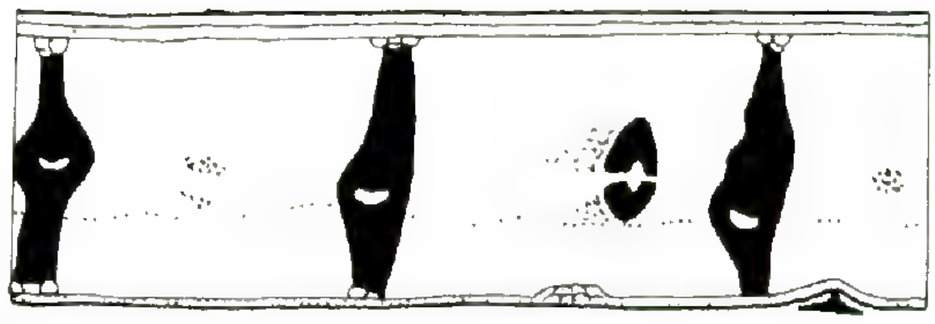

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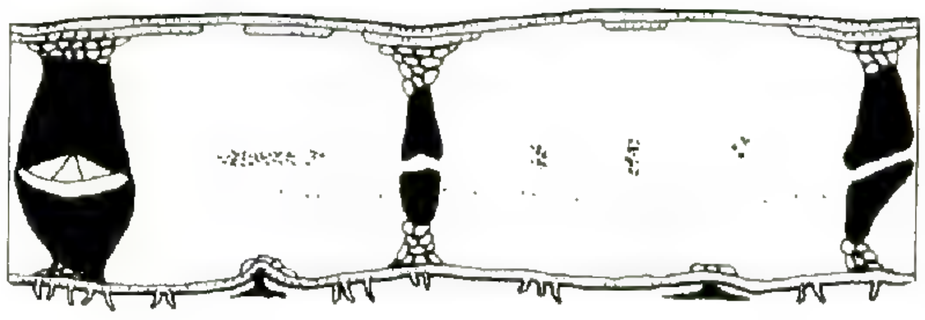

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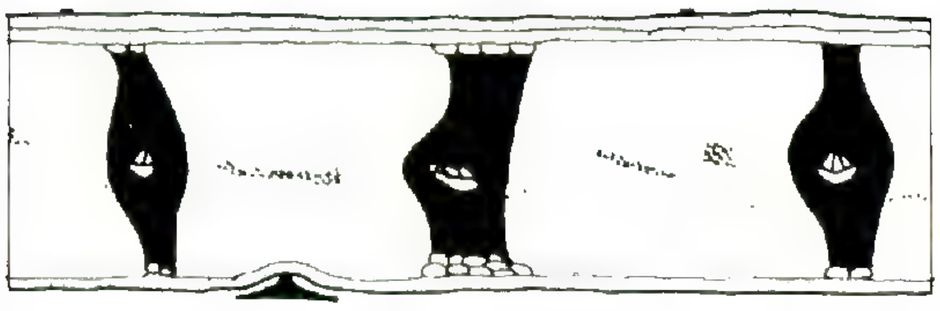

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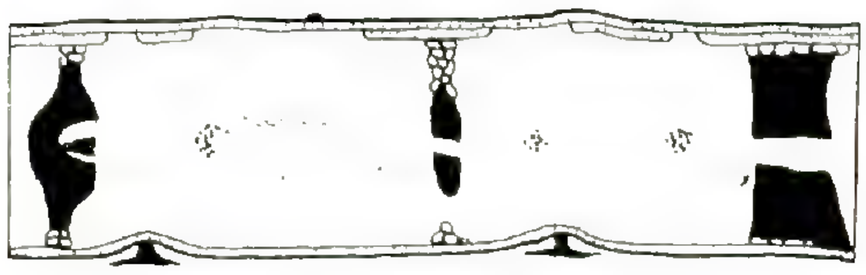

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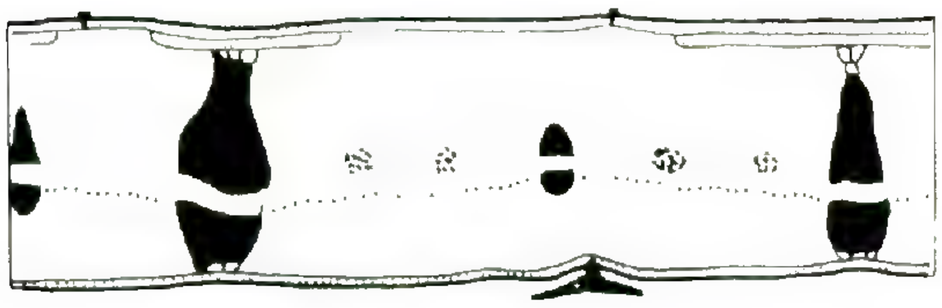

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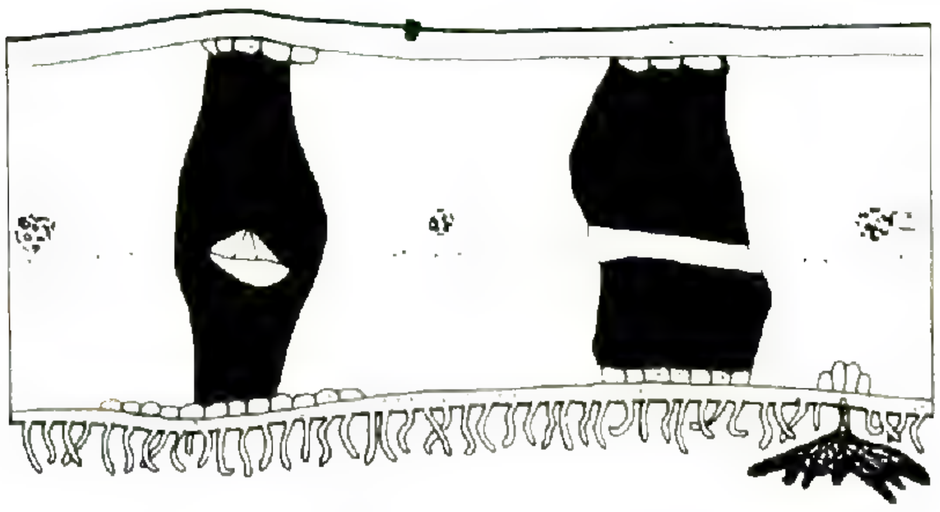

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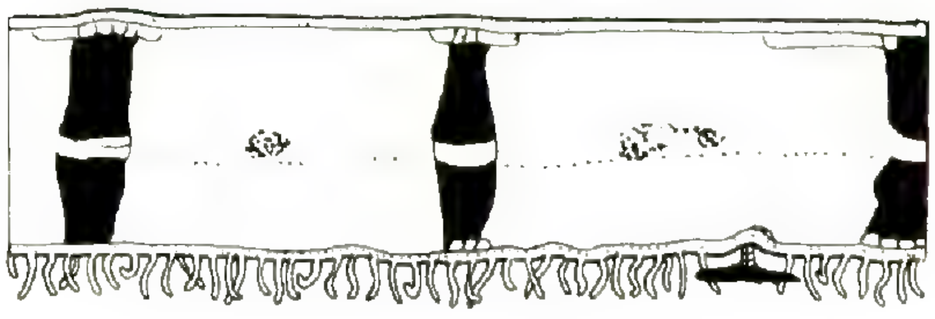

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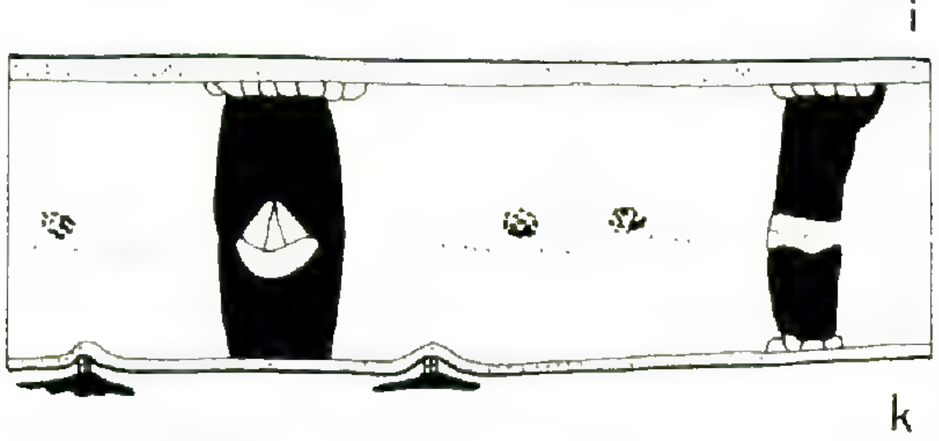

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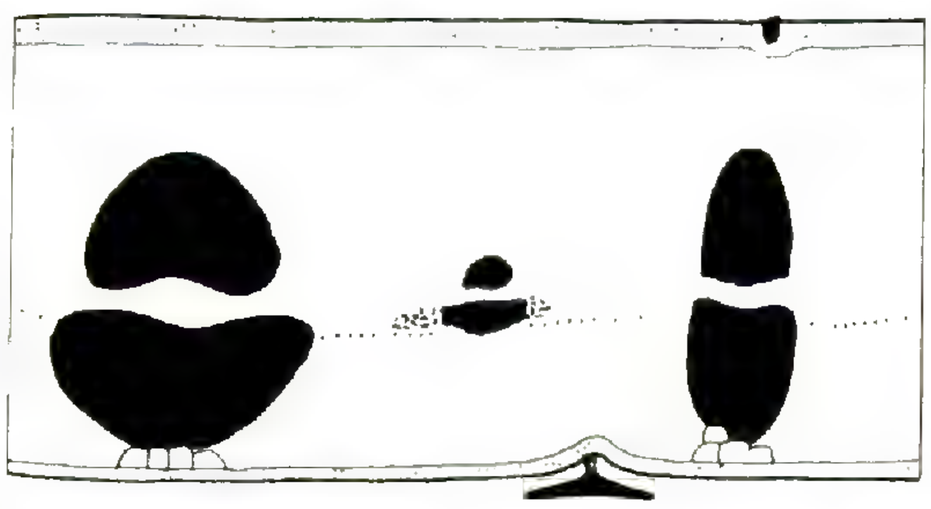

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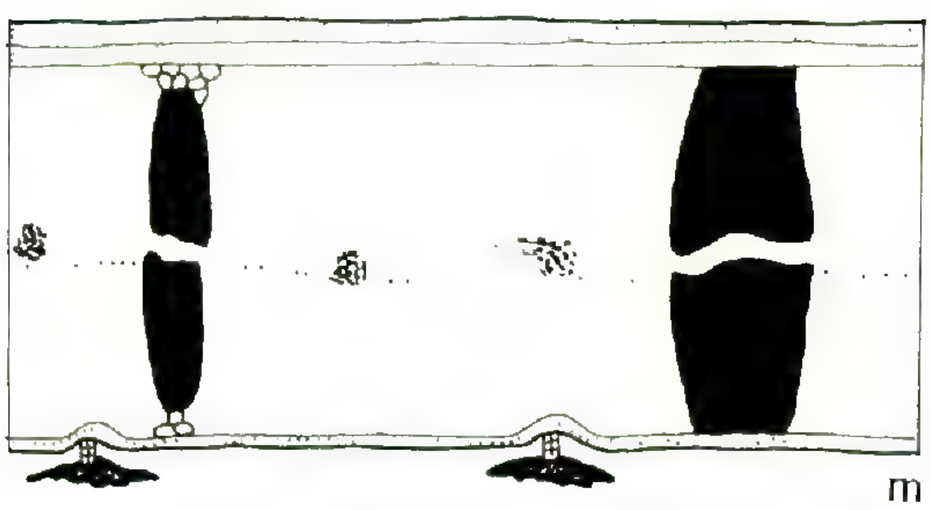

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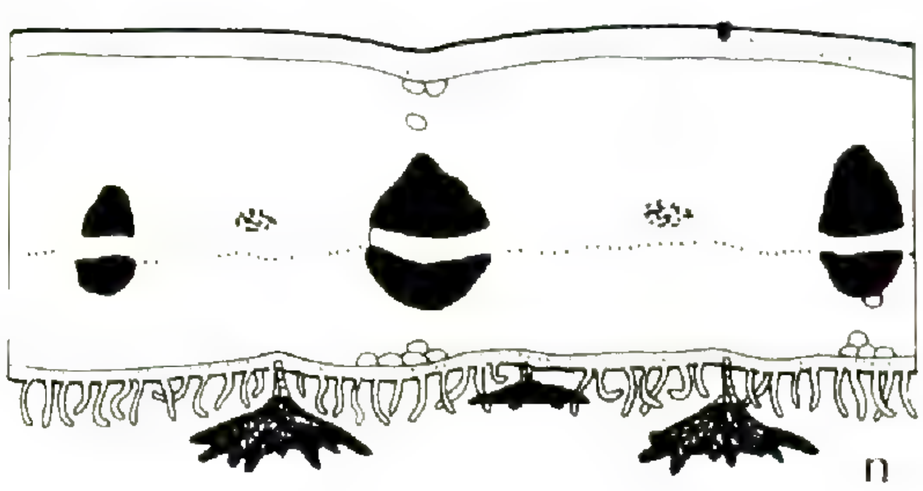

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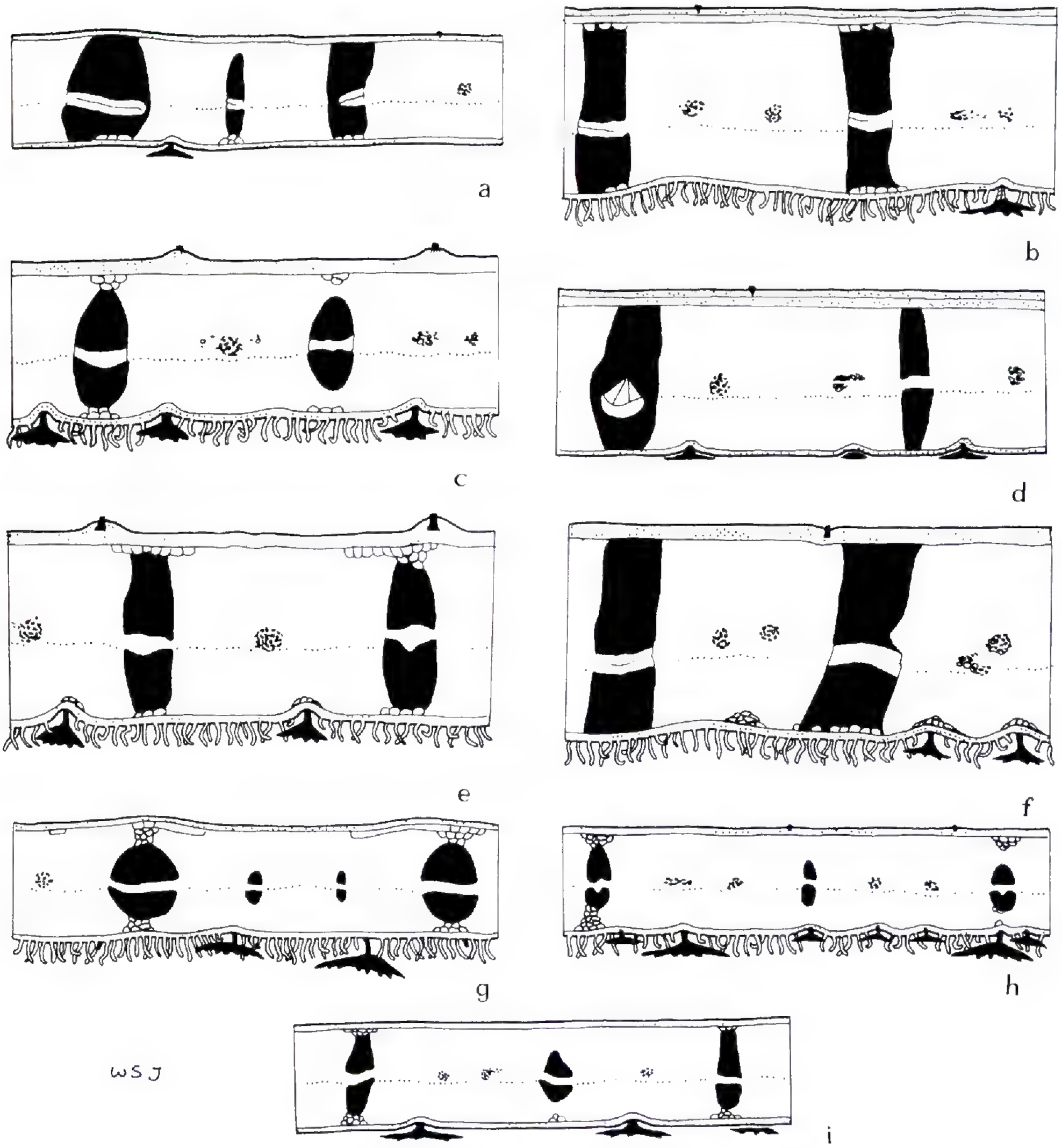
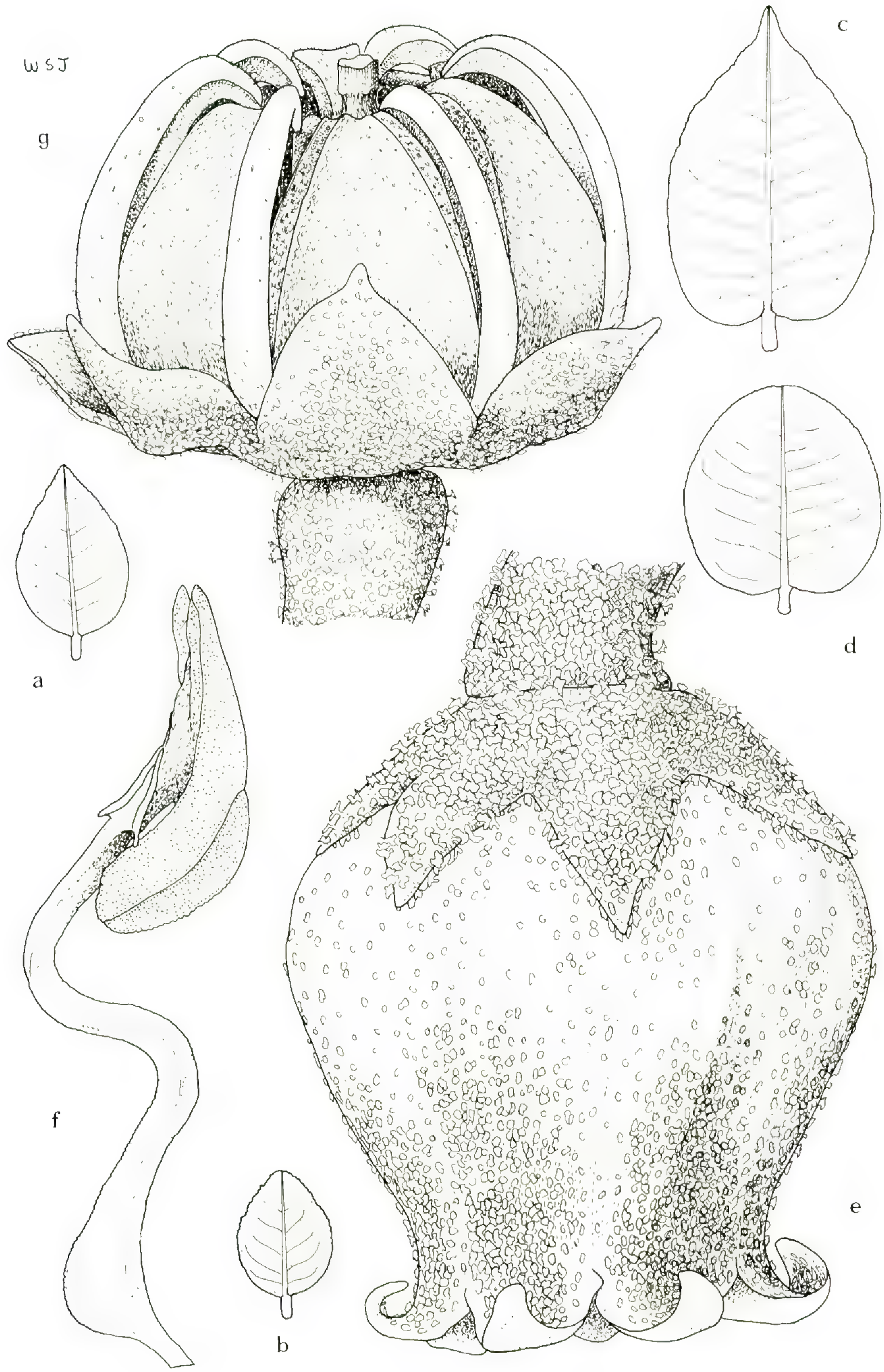


FIGURE 33. Cross sections of leaf blades of various species of *Lyonia* sect. LYONIA, × 50: a, *L. maestrensis;* b, *L. latifolia;* c, *L. glandulosa* var. *revolutifolia;* d, *L. myrtilloides;* e, *L. glandulosa* var. *glandulosa;* f, *L. toaënsis;* g, *L. fruticosa;* h, *L. ferruginea;* i, *L. squamulosa.*

FIGURE 32. Cross sections of leaf blades of various species of *Lyonia* sect. LYONIA, × 50: a, *L. tuerckheimii;* b, *L. rubiginosa* var. *stahlii;* c, *L. rubiginosa* var. *costata;* d, *L. rubiginosa* var. *rubiginosa;* e, *L. octandra;* f, *L. jamaicensis;* g, *L. trinidadensis;* h, *L. affinis;* i, *L. nipensis* var. *nipensis;* j, *L. elliptica;* k, *L. macrophylla;* l, *L. obtusa* var. *obtusa;* m, *L. ekmanii;* n, *L. nipensis* var. *depressinerva.*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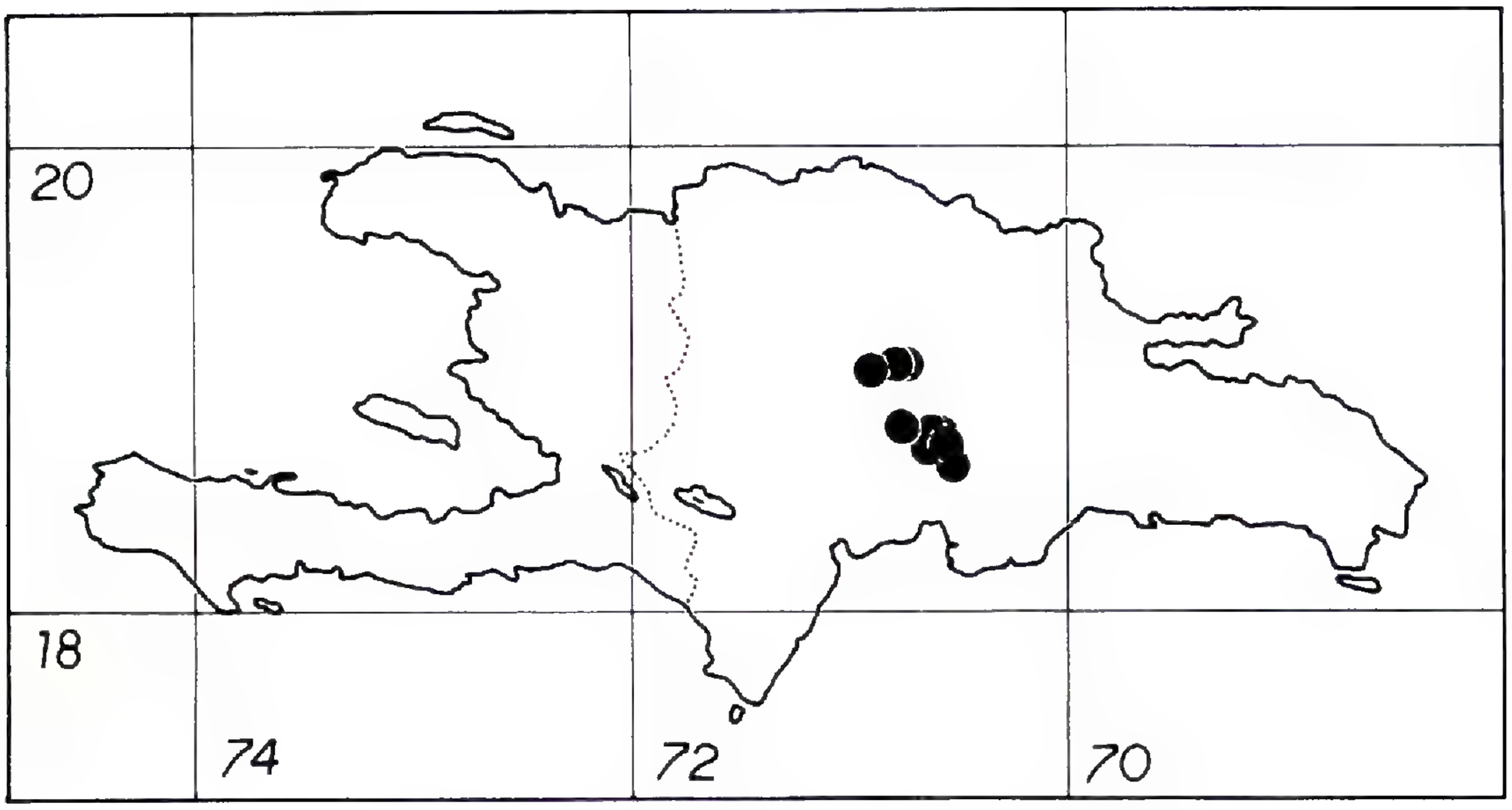


MAP 15. Distribution of *Lyonia heptamera*.

DISTRIBUTION AND ECOLOGY. Dominican Republic, Cordillera Central (MAP 15). Chiefly in high-elevation *Pinus occidentalis* forests, occasionally in adjacent cloud forests; ca. 2000–3175 m. alt. Common understory shrub, often occurring with clumps of *Danthonia domingensis* and shrubs such as *Lyonia tuerckheimii, L. urbaniana, Gaultheria domingensis, Baccharis myrsinites,* and *Pachyanthus urbanianus* (see also Urban, 1909, 1923; Graham & Jarzen, 1969; Liogier, 1976). Flowering ± continuously.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** ca. 11 km. above La Nuez, *D'Arcy 2671* (A); Sierra de Ocoa, San José de Ocoa, Loma Lucia, *Ekman H11695* (A, F, GH, S); Cordillera Central, Los Vallecitos del Yaque, *Ekman H13637* (NY, S); Valle Nuevo toward Sabana de la Vuelta, *Ekman H13895* (S); Loma Rosilla, *Fuertes 1765* (NY, P, US, W); La Lagunita, *Gastony et al. 298* (GH, NY, US); Pico Duarte, *Gastony et al. 358* (GH, NY, US); Valle Nuevo, near the "monument," *Judd 1182* (A); between Constanza and Valle Nuevo, *Judd 1216* (A); La Cotorra and La Rucilla, Ciénaga de Manabao, Jarabacoa, *Liogier 17195* (GH, US).

Lyonia heptamera is a very distinctive species that can be confused only with its close relative, *L. buchii,* from which it differs in its smaller, usually cordate-based, and more coriaceous leaves with more obscure venation on the adaxial surface, its urceolate flowers, and its low, shrubby habit (see FIGURE 36). In addition, the capsules of *L. heptamera* are chiefly six- and seven-merous, while those of *L. buchii* are more consistently six-merous. These two species are isolated by their elevational ranges and habitats, with

FIGURE 34. *Lyonia heptamera:* a–d, leaves, × .5; e, flower, × 6; f, stamen, × 12.5; g, capsule, × 6.

TABLE 10. **Morphological comparison of species and hybrids of high-elevation pine forests of the Cordillera Central, Dominican Republic.**

CHARACTER	TAXON					
	L. urbaniana	Hybrid between *L. urbaniana* and *L. heptamera*	*L. heptamera*	Hybrid between *L. heptamera* and *L. tuerckheimii*	*L. tuerckheimii*	Hybrid between *L. tuerckheimii* and *L. urbaniana*
Habit	Shrub to ca. 3.5 m. tall	Shrub to ca. 3.5 m. tall	Shrub to ca. 2 m. tall	Shrub to ca. 2 m. tall	Shrub to ca. 2(–2.5) m. tall	Shrub to ca. 2 m. tall
Twigs	Slender	Stout to slender	Stout	Stout	Stout	Slender
Lamina						
Shape	Ovate	Ovate	Ovate	Ovate	Elliptic to ovate (or obovate)	Ovate (to elliptic)
Length (cm.)	1–2.5(–3)	2–4.7	2–6(–9)	2.5–4.7	1.8–5(–6.5)	2–5
Width (cm.)	0.7–1.7(–2.5)	1.3–3.5	1.7–5(–6.7)	1.6–3.5	0.8–2.5(–3.6)	1–2.8
Base	Broadly cuneate to rounded	Slightly cordate to broadly cuneate	Cordate to rounded	Broadly cuneate to slightly cordate	Narrowly cuneate to rounded	Rounded to broadly cuneate
Margin	Usually strongly toothed	Obscurely to strongly toothed	Undulate to obscurely toothed	Obscurely to strongly toothed	Strongly to obscurely toothed	Usually strongly toothed
Veins (abaxial surface)	Raised (fine reticulum)	Moderately raised (clear reticulum)	Prominently raised (coarse reticulum)	Slightly raised (obscure reticulum)	± Flat	± Flat to slightly raised (fine and obscure reticulum)

Texture (adaxial surface)	Roughened	Roughened	± Roughened	Smooth to roughened	Smooth	Smooth to very slightly roughened
Unicellular hairs (abaxial surface)	Dense	Dense	Dense	Dense	Lacking	Sparse to moderate
Petiole length (mm.)	1–4	(3–)4–7(–9)	4–10	2.5–8	2.6–6(–8)	3–5
Pedicel length (mm.)	2–6	8–13	5–20	6–11	4–13(–17)	Ca. 8
Merosity	4 or 5	5 or 6	(5 or) 6 or 7 (or 8)	5 or 6	5 (or 6)	5
Calyx length (mm.)	0.9–2	2–3.5	2.5–6	1.5–2.3	1.2–2	Ca. 1
Corolla						
Shape	Cylindrical	Urceolate	Urceolate	Cylindrical to long-urceolate	Cylindrical	----
Length (mm.)	3–5.5	Ca. 6	8–13	8–10	(5.5–)6.5–10	----
Width (mm.)	2–3	Ca. 4.5	8–13	5.5–7.5	(2.5–)3–4.5	----
Pubescence	Sparsely lepidote	Densely to moderately lepidote	Densely to moderately lepidote	Moderately lepidote	Sparsely lepidote	----
Capsule						
Length (mm.)	2.5–5	3–5	4–7	----	4–7	Ca. 4
Width (mm.)	1.5–3.5	5–6	7–10.5	----	3–5	Ca. 3.5

L. heptamera essentially limited to high-elevation pine forests (ca. 2000–3175 m. alt.), and *L. buchii* occurring chiefly in low-elevation pine forests, cloud forests, and thickets (ca. 800–2100 m. alt.; FIGURE 5). Although their elevational ranges appear to overlap slightly, the two taxa have not been seen growing together (pers. obs.).

Vigorous young shoots of both species are often bright orange due to their dense covering of peltate scales, and the leaves are often colored reddish by anthocyanin pigments. As the leaves become lignified, their color changes to a deep green. The size of the leaves and the depression of the secondary through quaternary veins on the adaxial surface varies greatly with the vigor and habitat of the shrub. Young plants or seedlings have much smaller, less raised-reticulate–veined, more cuneate-based, ovate leaves with fewer unicellular hairs on the abaxial surface than do mature plants. As the shrubs increase in size, the leaves become cordate based. In many shrubs both leaf types can be found: cordate-based on upper erect shoots and cuneate-based on small shoots near the base of the plant.

Since *Lyonia heptamera* flowers more or less continuously throughout the year, it is often in bloom at the same time as *L. tuerckheimii* and *L. urbaniana*, which grow in the same habitats, and there are occasional hybrids between it and these two species. The presumed hybrid *Lyonia heptamera* × *urbaniana* was first collected by E. L. Ekman in 1929 near Valle Nuevo. He stated on the specimen label that "It grew together with its supposed parents, and nearly sterile. Afterwards I have, however, seen isolated plants of it elsewhere!" This collection (*Ekman H13860*) is the type of *Xolisma cryptogonia* Sleumer (Repert. Spec. Nov. **36:** 270, 271. 1934), which was transferred to *Lyonia* by Jiménez (Rhodora **62:** 237. 1960). Sleumer (1934, p. 271) stated that: "Ein Teil des Materials (1. folia ovata vel breviter ovata) steht der *X. heptamera* näher, ein weiterer Teil (2. folia ovato-elliptica) dürfte zwischen den vermeintlichen Eltern die Mitte halten, vier kleine Zweige mit ebenso langen, aber mehr zugespitzten Blättern (3. folia ovato-acuminata) neigen zu *X. Urbaniana.*" Although this description might lead one to suspect that the material was collected from a hybrid swarm, the differences between the various branches comprising the type collection are not much more than what has been found to be the normal range of variation in isolated populations of *L. heptamera.* Not only, as discussed earlier, is there much variation in type of leaf base in this species, but leaves from the same plant can be acute, acuminate, or truncate to rounded, and they are occasionally quite reduced in size toward the tips of some branches (see *Judd 1214, 1224, 1225, 1227, 1305,* all at A). In the Valle Nuevo area, plants (e.g., *Judd 1234,* A) that appeared to be F_1 hybrids between *L. heptamera* and *L. urbaniana* have only very rarely been found, and no populations have been discovered in which the variation observed could be explained by the backcrossing of hybrids to the parental species (pers. obs.). The hybrid is essentially intermediate in all its characters (see TABLE 10).

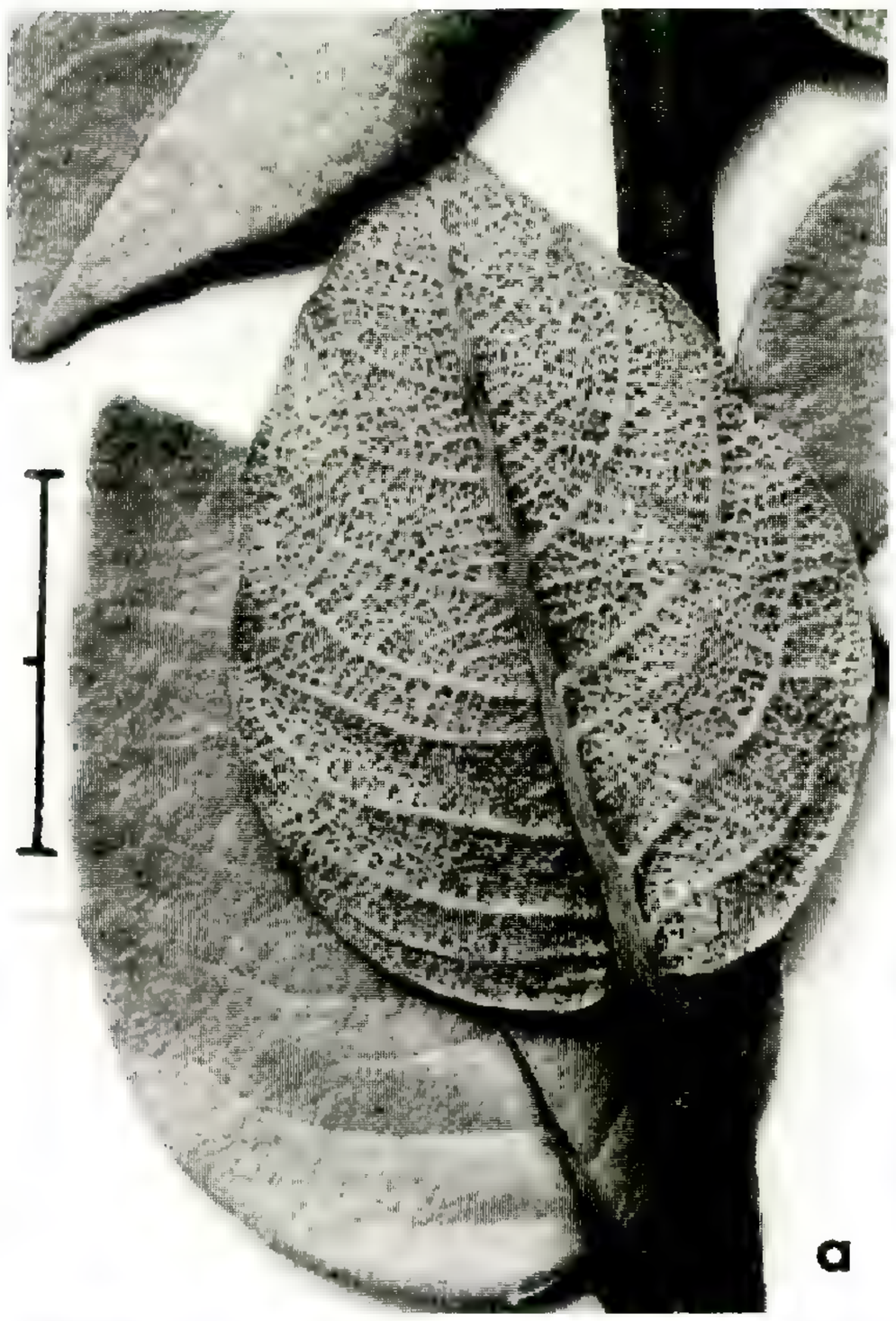
The capsules present on *Ekman H13860* contain seeds, several of which are shrunken, but many seeds fail to develop fully even in normal plants. Unfortunately, all of the presumed hybrid plants observed in the field were

in vegetative condition. More work is needed here. The flowers of *Lyonia heptamera* are approximately three times as large as those of *L. urbaniana;* thus the scarcity of hybrids might be explained by different insects pollinating the two species.

Although *Lyonia tuerckheimii* is more abundant than *L. urbaniana* and can frequently be found growing with *L. heptamera,* hybrids between these two species are quite rare. Presumed hybrids have only been seen in the high-elevation pine forest near Valle Nuevo (*Jiménez & Lithgow 1392* (US); *Judd 1230* (A)). Near Valle Nuevo one plant was found that was perfectly intermediate between *L. heptamera* and *L. tuerckheimii* and was growing with them in an open, burned-over area. Again, pollinator differences (the flowers of *L. tuerckheimii* are cylindrical and are about half as wide as those of *L. heptamera*) may help to keep these two taxa isolated. The hybrid seems to be partially sterile; the one flowering specimen seen had approximately 40 percent of its pollen tetrads at least partially collapsed or unstained with cotton blue in lactophenol, so there may be partial genetic barriers isolating the two species. The morphological characteristics of these hybrids are listed in TABLE 10.

10. **Lyonia buchii** Urban, Symb. Antill. **8:** 515. 1920. TYPE: Haiti, in monte Brouet, 1800 m. alt., September 1919, *W. Buch 1699* (holotype, B (destroyed); isotypes, GH!, IJ!).

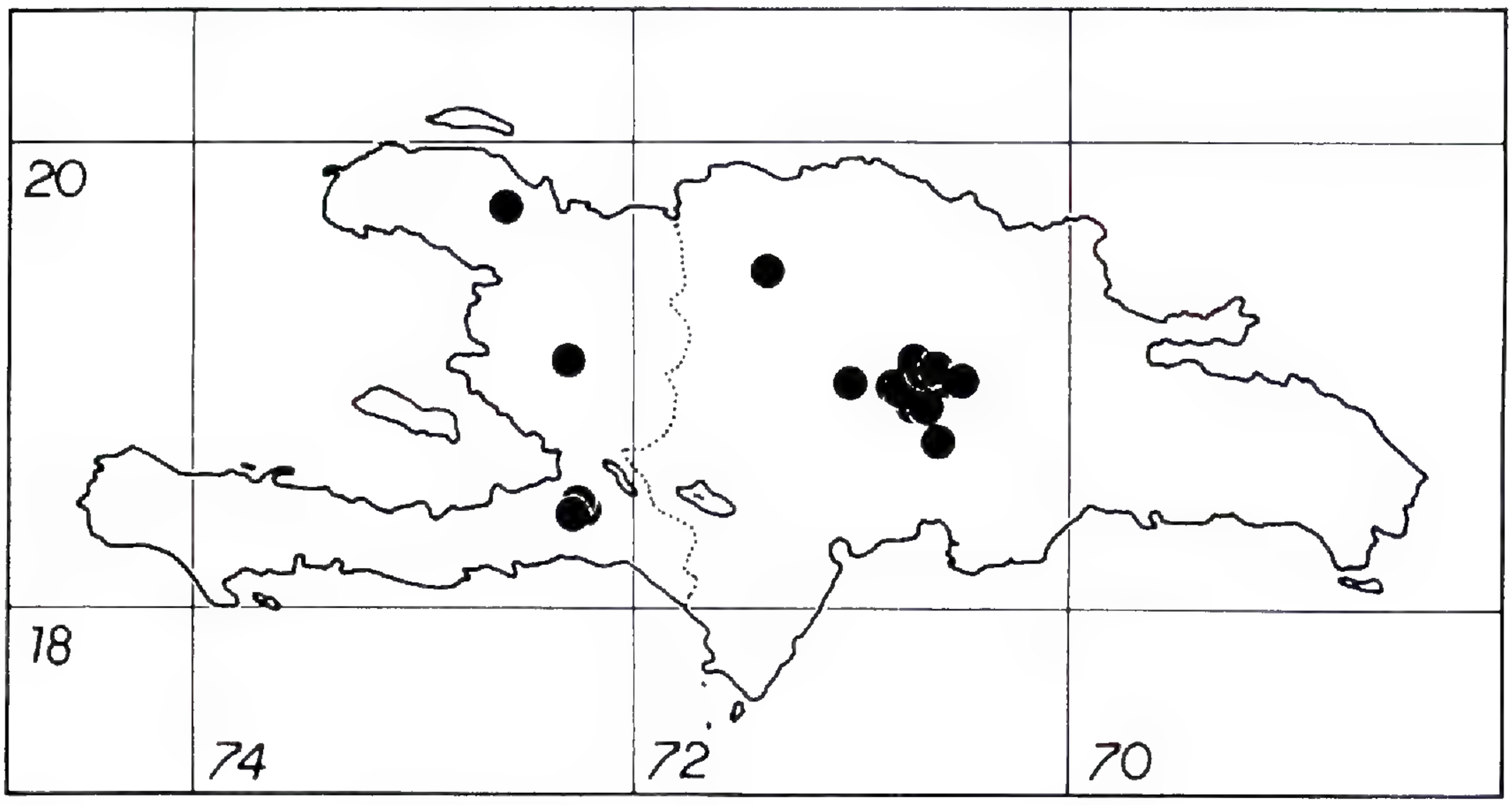
Evergreen, erect shrub to medium-sized tree to ca. 6 meters tall, with gray, longitudinally furrowed, somewhat shredding bark. Twigs slightly angled, slender, sparsely to moderately lepidote, otherwise glabrous. Buds ovoid, 1.2–3.5 by 1–2.5 mm. Leaf blades elliptic to ovate, (2.5–)3.5–10(–14) by 2–7(–9) cm., ± flat, coriaceous, ca. 0.25–0.45 mm. thick; apex acute or acuminate to rounded; base rounded to narrowly cuneate; margin plane to slightly revolute, distal portion irregularly undulate to obscurely and irregularly toothed, proximal portion undulate to entire; venation brochidodromous, 3° veins percurrent to reticulate; adaxial surface lepidote but scales usually quickly deciduous, glabrous on midvein, with all veins clearly slightly depressed; abaxial surface moderately to densely lepidote, otherwise densely pubescent, with all veins prominently raised and forming conspicuous network; scales rust colored, deciduous to persistent, ca. 0.08–0.34 mm. in diameter, erose to nearly entire; petiole 5–13 mm. long, lepidote, otherwise glabrous. Flower buds above or intermixed with vegetative buds; inflorescences shortly racemose to fasciculate, 4- to 10-flowered. Pedicels clearly articulated with calyx, stout, 4–13(–25) mm. long, lepidote, otherwise glabrous or less commonly sparsely pubescent; bracteoles opposite or subopposite, basal or nearly so, narrowly triangular, 1.5–3 mm. long; bracts to ca. 5 mm. long, usually caducous. Flowers (5- or) 6- (or 7-)merous; calyx lobes triangular, with acute to acuminate apices, 2.5–4.5 by 1.5–2.5 mm., the adaxial side sparsely pubescent near margins, the abaxial side densely lepidote, otherwise sparsely or moderately pubescent; corolla carnose, widely urceolate to campanulate, 6–10 by 7–11


a

b

c

d



MAP 16. Distribution of *Lyonia buchii*.

mm., white, abaxially densely to moderately lepidote; filaments roughened, 3.5–5 mm. long, unappendaged or with poorly developed spurs to ca. 0.2 mm. long near junction with anthers, anthers 1.5–2 mm. long; ovary lepidote, otherwise pubescent, placentae subapical. Capsule subglobose to short-ovoid, (3–)3.5–6 by 5.5–9 mm., lepidote, otherwise sparsely to densely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–3.5 mm. long. (FIGURES 35, 37.)

DISTRIBUTION AND ECOLOGY. Hispaniola, Cordillera Central (including Massif du Nord), Massif de la Selle, and Massif des Cahos (MAP 16). Chiefly in thickets, cloud forests, and low-elevation *Pinus occidentalis* forests; 800–2100 m. alt. Locally common in low-elevation *Pinus occidentalis* forests of Cordillera Central and in lush, cloud-forest zone at slightly higher elevations between Valle Nuevo and Constanza. Flowering ± continuously.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Dos Ríos to Banao, *Bro. Augusto 1234* (A, NY); 13.5 km. W. of Duarte Hwy. on rd. to El Río, *D'Arcy 2591* (A); Cordillera Central, Monción, Lagunas de Cenobi, *Ekman H12880*

FIGURE 35. a, *Lyonia heptamera* (*Gastony et al. 298*, NY): note prominent raised-reticulate pattern of venation on abaxial leaf surface. b, *L. buchii* (*Ekman 3691*, S): note prominent raised-reticulate veins on abaxial leaf surface; tertiary, quaternary, and even higher order veins visible and slightly depressed on adaxial surface. c, *L. urbaniana* (*Liogier 13119*, NY): note roughened leaf epidermis on adaxial surface; leaves clearly toothed and with dense, fine, raised-reticulate network of veins on abaxial surface (just visible as small light and dark patches in photo, obscured by dense layer of peltate scales). d, *L. tinensis* (*Ekman 14019a*, K): note smooth adaxial leaf epidermis. Scale = 2 cm.

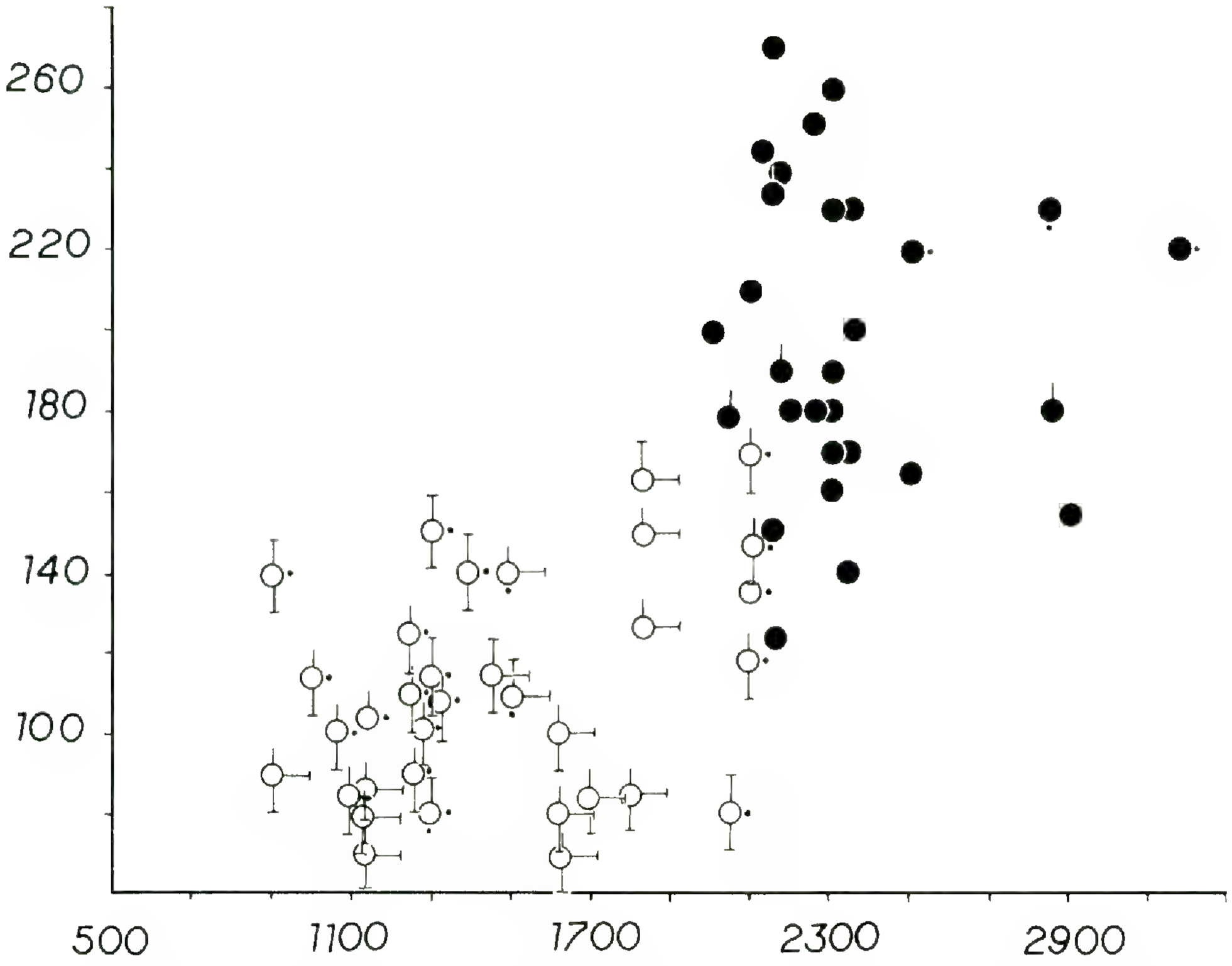


FIGURE 36. Scatter diagram showing variation between *Lyonia heptamera* and *L. buchii* in six characters. Vertical axis = leaf-base angle in degrees (3rd leaf from branch apex); horizontal axis = elevation in meters; closed circle = high-order leaf veins ± obscure on adaxial surface, open circle = leaf veins prominent on adaxial surface; tail to right = corolla ± campanulate, no tail to right = corolla urceolate; tail down = tree above 2 m., no tail down = shrub of 2 m. or less; full tail up = largest leaf greater than 10 cm. long, half tail up = largest leaf 6–10 cm., no tail up = largest leaf less than 6 cm. Small dots indicate character could not be scored.

(S); La Ciénaga, N. of Constanza, *Jiménez 4004* (US); between El Río and El Salto, *Judd 1138* (A); between Constanza and Valle Nuevo, *Judd 1193* (A); between "the monument" near Valle Nuevo and La Nuez, *Judd 1196* (A); S. of Jarabacoa, Loma de la Sal, *Judd 1399* (A); Ciénaga de Manabao, Loma entre los Ríos, Jarabacoa, *Liogier 12100* (GH, NY); Alto Casabito, above Banao, *Liogier 14748* (NY); La Nevera, Valle Nuevo, *Liogier 20680* (JMB, NY); between La Culata and La Ciénaga, Constanza, *Liogier & Liogier 22228* (JMB). **Haiti:** ridge between Morne Tranchant and Morne Brouet, slope of Rivière Thébaud, *Ekman H1221* (S, US); Massif de la Selle, Furcy, at Rivière Thébaud, *Ekman H3236* (A, F, GH, S, US); Massif des Cahos, Petite-Rivière de l'Artibonite, Pérodin, *Ekman H3417* (NY, S); Massif du Nord, Port de Paix, Haut-Piton, *Ekman H3691* (S); between Kenscoff and Furcy, *Proctor 10899* (IJ, US).

Lyonia buchii is a very distinct species that can be confused only with its close relative, *L. heptamera,* from which it differs in its larger leaves

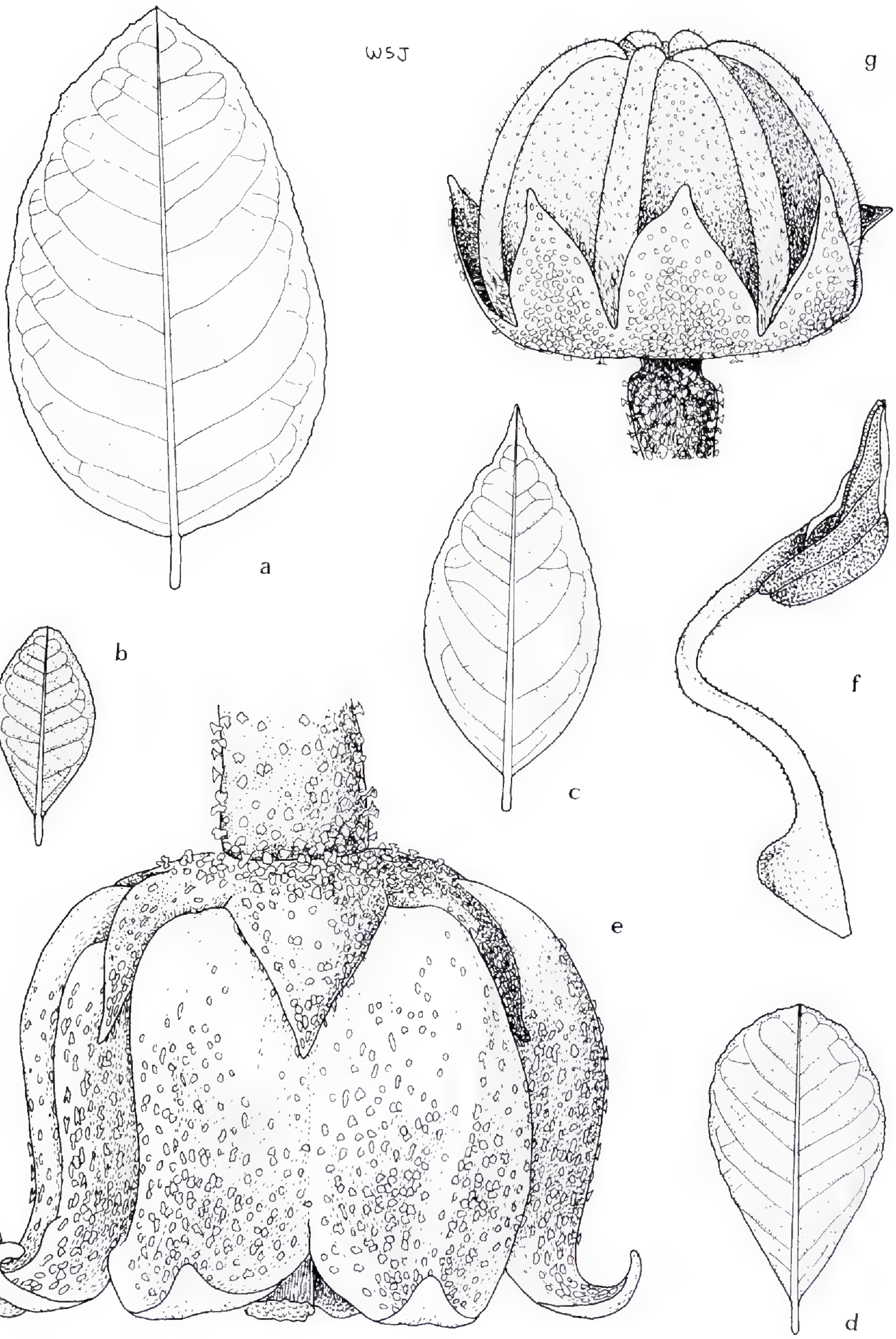


FIGURE 37. *Lyonia buchii:* a–d, leaves, × .5; e, flower, × 6; f, stamen, × 12.5; g, capsule, × 6.

with cuneate to rounded bases and clearly evident, depressed, higher order veins on the adaxial surfaces, its widely urceolate to campanulate flowers, and its more upright, aborescent habit (FIGURE 36). Plants producing some cordate leaves (e.g., *Judd 1196*) have been collected near the upper limits of the elevational range of *L. buchii* and possibly indicate some hybridization with *L. heptamera*. However, these two taxa have not as yet been found growing together, and in other characters these unusual plants agree well with *L. buchii*.

The size of leaves in otherwise identical plants can vary greatly with the vigor of the shrub and its habitat (see FIGURE 37). Small- and large-leaved

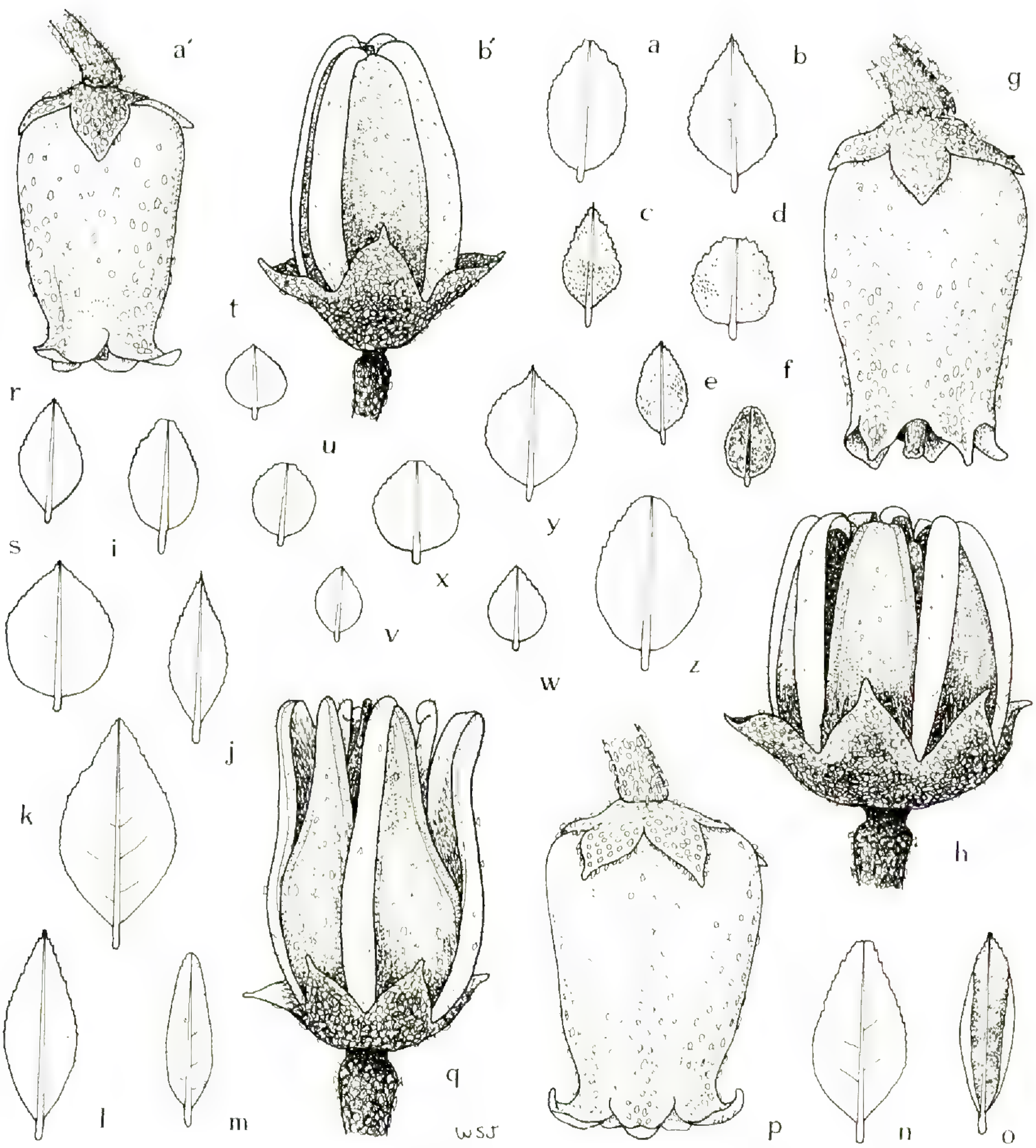
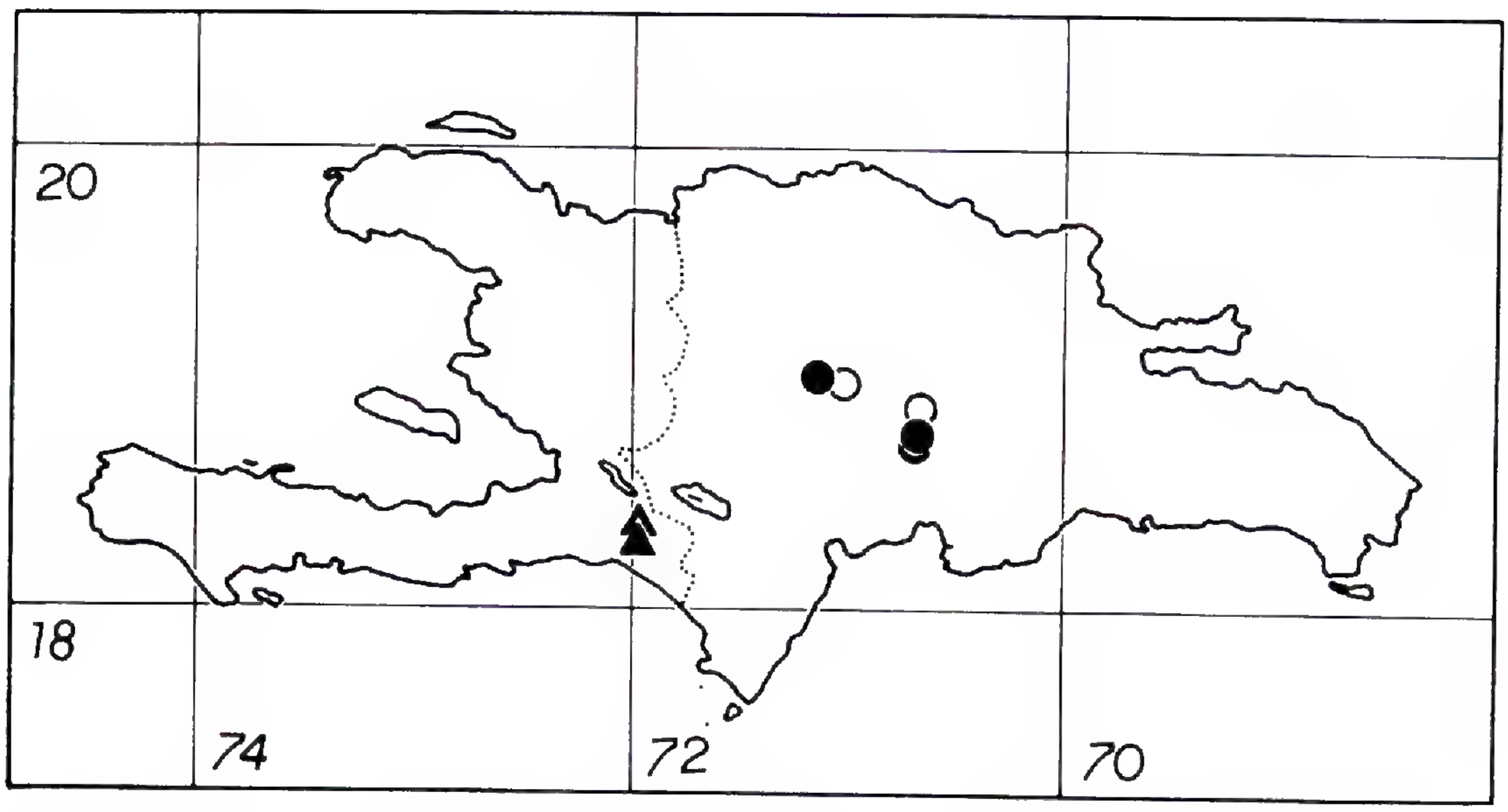


FIGURE 38. a–h, *Lyonia urbaniana:* a–f, leaves, × .5; g, flower, × 6; h, capsule, × 6. i–q, *L. tinensis:* i–o, leaves, × .5; p, flower, × 6; q, capsule, × 6. r–b′, *L. microcarpa:* r–z, leaves, × .5; a′, flower, × 6; b′, capsule, × 6.



MAP 17. Distribution of *Lyonia urbaniana* (dots), *L. alpina* (triangles), and *L. alainii* (circles).

plants can sometimes occur together, and herbarium specimens of such small-leaved plants (e.g., *Judd 1196* and *1399*, and *Liogier 20680*) can cause problems in identification.

11. **Lyonia urbaniana** (Sleumer) Jiménez, Rhodora **62:** 237. 1960.

Xolisma urbaniana Sleumer, Repert. Sp. Nov. **36:** 273. 1934. TYPE: Dominican Republic, Cordillera Central, Prov. de la Vega, Valle Nuevo, toward Sabana de la Vuelta, ca. 2400 m., 29 October 1929, *E. L. Ekman H13861* (holotype, S!; isotypes, GH!, NY!, S!).

Evergreen, erect shrub to ca. 3.5 meters tall, with gray, longitudinally furrowed bark. Twigs slightly angled, slender, moderately to densely lepidote, otherwise glabrous. Buds ovoid, 1–2 by ca. 1 mm. Leaf blades ovate, 1–2.5(–3) by 0.7–1.7(–2.5) cm., ± flat, coriaceous, ca. 0.35–0.45 mm. thick; apex acute to truncate; base broadly cuneate to rounded; margin plane to slightly revolute, distal portion usually strongly and irregularly toothed, proximal portion obscurely toothed to entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface roughened by thickened scale bases, lepidote but scales usually quickly deciduous, usually sparsely pubescent on proximal portion of midvein, with 2° and higher order veins obscure (rarely 2° veins very slightly depressed); abaxial surface moderately to densely lepidote, otherwise densely pubescent, with all veins raised to form dense, fine reticulum, often not visible without magnification; scales usually brown to dark brown, usually ± persistent, ca. 0.07–0.27 mm. in diameter, erose; petiole 1–4 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 4- to 8-flowered. Pedicels clearly articulated with calyx, slender, 2–6 mm. long, lepidote, otherwise glabrous; bracteoles

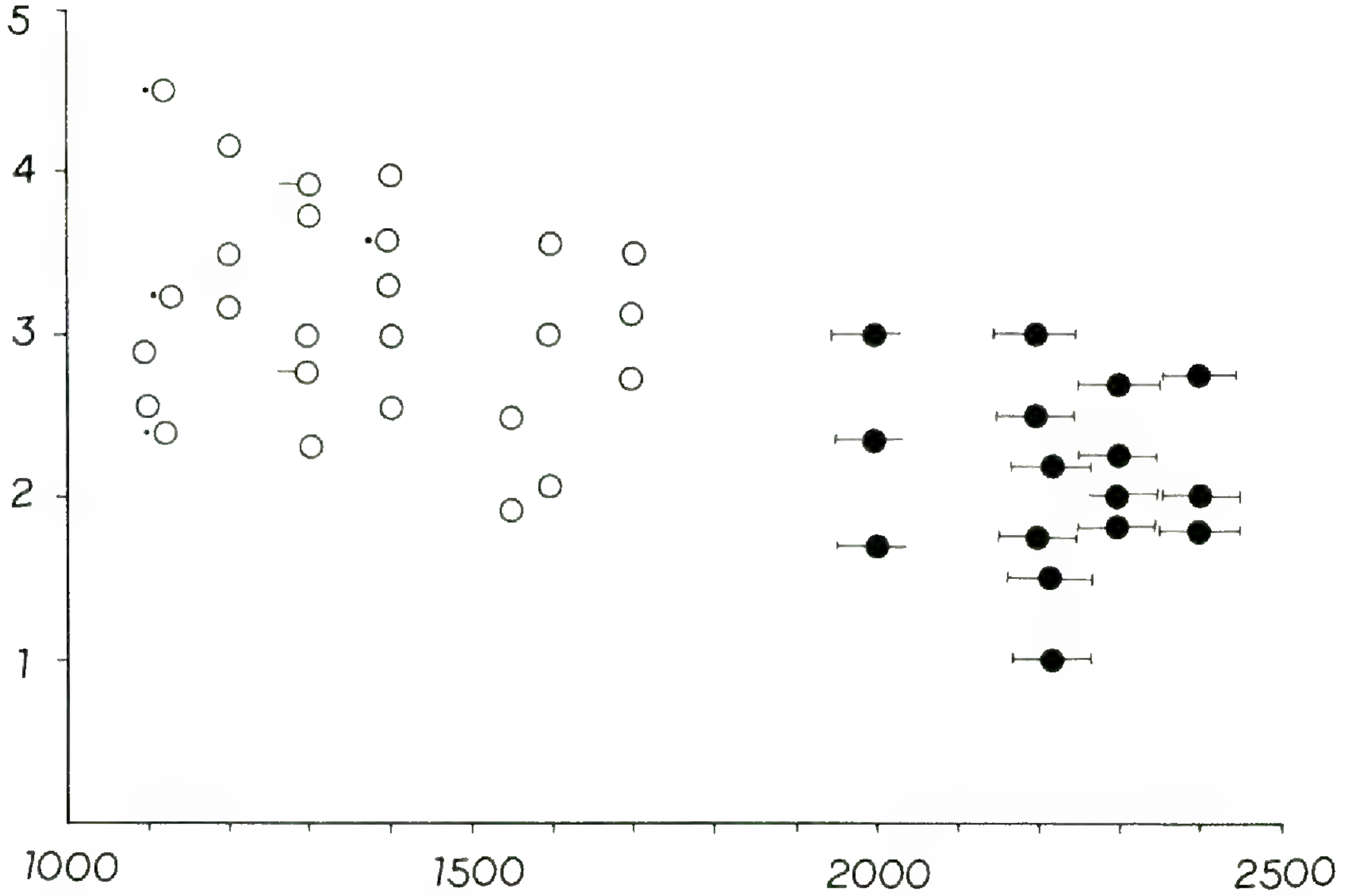


FIGURE 39. Scatter diagram showing variation between *Lyonia urbaniana* and *L. tinensis* in five characters. Vertical axis = leaf length in cm. (3rd or 4th leaf from branch apex); horizontal axis = elevation in meters; solid circle = adaxial leaf surface roughened, open circle = adaxial leaf surface ± smooth; full tail to left = capsule not constricted at apex, no tail to left = capsule with constricted apical portion, half tail to left = intermediate; full tail to right = leaves densely covered with brown scales on abaxial surface (at least when young), no tail to right = leaves sparsely to moderately covered with tan to light brown scales, half tail to right = intermediate. Small dots indicate character could not be scored.

opposite, basal, narrowly triangular, 1–1.5 mm. long; bracts to ca. 2 mm. long. Flowers 4- or 5-merous; calyx lobes triangular, with acuminate apices, 0.9–2 by 0.7–1 mm., the adaxial side sparsely pubescent at margins and near apex, the abaxial side lepidote, otherwise glabrous; corolla cylindrical, 3–5.5 by 2–3 mm., white, abaxially sparsely lepidote; filaments roughened, 2.5–3 mm. long, unappendaged, anthers 0.8–1 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsules ovoid to narrowly ovoid or less commonly ellipsoid, 2.5–5 by 1.5–3.5 mm., apex not constricted, slightly lepidote, otherwise sparsely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.7–2.5 mm. long. (FIGURES 35, 38.)

DISTRIBUTION AND ECOLOGY. Dominican Republic, Cordillera Central (MAP 17). High-elevation *Pinus occidentalis* forests, ca. 2000–2400 m. alt. Locally common understory shrub among clumps of *Danthonia domingensis*. Seldom collected in flower but probably blooming chiefly in spring.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** SAN JUAN: Sabana Nueva, Piedra del Aguacate to Río del Oro, *Howard & Howard 9097* (GH, NY, S, US, USD). LA VEGA: Valle Nuevo, *Jiménez 2548* (HJ, US); N. of Valle Nuevo, *Judd 1233* (A); Valle Nuevo, *Liogier 13119* (A, IJ, JMB, NY).

Lyonia urbaniana is closely related to *L. tinensis* and *L. microcarpa.* It differs from *L. tinensis* in its smaller leaves with roughened (vs. ± smooth) adaxial surfaces and its ovoid, four- or five-merous capsules lacking a constricted apex (Figures 38, 39) (vs. five-merous, narrowly ovoid capsules with a slightly constricted apex); and from *L. microcarpa* in its leaves that are longer in relation to their width and that have brownish (vs. ± orange) scales, its often larger corollas, and its ovoid, wider, and more often five-merous (vs. small, narrowly ovoid, usually four-merous) capsules (FIGURE 38). Some plants with extremely truncate leaves approach *L. microcarpa* in leaf length/width ratio (see *Judd 1235*). *Lyonia urbaniana* is geographically isolated from *L. microcarpa,* since the former occurs in the Cordillera Central, while the latter is found only in the Massif de la Selle–Sierra de Baoruco. It is isolated from *L. tinensis* by habitat and elevational range: *L. urbaniana* occurs in high-elevation pine forests and savannas above ca. 2000 meters altitude, and *L. tinensis* in low-elevation pine forests ca. 1100–1700 meters altitude (FIGURE 5 and MAP 18).

Lyonia urbaniana can be found growing with *L. heptamera* and *L. tuerckheimii* and occasionally hybridizes with both of these quite distinctive taxa in the Valle Nuevo area (*Judd 1226a* (A), *1233a* (A)). Neither of these putative hybrids is very common, however, and no evidence of backcrossing or further hybridization has been discovered. The major morphological characteristics of both hybrids are given in TABLE 10.

12. **Lyonia tinensis** Urban, Symb. Antill. **7:** 533. 1913.

Xolisma tinensis (Urban) Small, N. Am. Fl. **29**(1)**:** 70. 1914. TYPE: Dominican Republic, prov. de Azua, in Placer de la Tina, 1600 m. alt., July 1912, *Fuertes 1917* (holotype, B (destroyed); isotypes, L!, NY!, P!, US!, USD!, W!).

Xolisma pseudotinensis Sleumer, Repert. Sp. Nov. **36:** 272. 1934. *Lyonia pseudotinensis* (Sleumer) Jiménez, Rhodora **62:** 237. 1960. TYPE: Dominican Republic, Cordillera Central, prov. la Vega, Constanza, Gajo de la Angostura, ca. 1300 m. alt., 6 November 1929, *E. L. Ekman H14019b* (holotype, S!; isotypes, A!, GH!, NY!).

Evergreen, usually erect shrub or small tree to 5 meters tall, with grayish, longitudinally furrowed bark. Twigs slightly angled, slender, sparsely to densely lepidote, otherwise glabrous to sparsely pubescent. Buds ovoid, 1–2 by 0.8–1.3 mm., lepidote. Leaf blades ovate to elliptic, 1.7–3.5(–4.7) by 0.9–1.9(–2.8) cm., flat to moderately recurved, coriaceous, ca. 0.32–0.45 mm. thick; apex slightly acuminate to truncate; base cuneate to rounded; margin plane to slightly revolute, distal portion strongly to obscurely and irregularly toothed (rarely nearly entire), proximal portion strongly toothed to entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, moderately to sparsely pubescent on proximal

portion of midvein, 2° and 3° veins obscure to slightly visible, few 2° veins sometimes depressed; abaxial surface sparsely to moderately lepidote, otherwise densely pubescent, with all veins raised, forming dense and fine reticulum, often not visible without magnification; scales usually light brown, often becoming whitish, persistent to less commonly deciduous, ca. 0.08–0.26 mm. in diameter, erose; petiole 2–4.5 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 3- to 10-flowered. Pedicels clearly articulated with calyx, slender, (2.5–)3–7.5 mm. long, lepidote, otherwise glabrous; bracteoles ± opposite, basal, narrowly triangular, 1–1.3 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5-merous; calyx lobes triangular, with acuminate apices, 0.7–1.5 by 0.6–0.9 mm., the adaxial side sparsely pubescent at margins and near apex, the abaxial side lepidote, otherwise glabrous; corolla cylindrical, 4–5 by 2–3 mm., white, abaxially sparsely lepidote; filaments roughened, 2.5–3 mm. long, unappendaged, anthers 0.8–1 mm. long; ovary lepidote, otherwise pubescent, placentae subapical. Capsules usually ovoid, 3.5–6 by 1.5–3 mm., apex usually slightly constricted, slightly lepidote, otherwise sparsely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1–2.9 mm. long. (FIGURES 35, 38.)

DISTRIBUTION AND ECOLOGY. Dominican Republic, Cordillera Central (MAP 18). Low-elevation *Pinus occidentalis* forests, ca. 1100–1700 m. alt. Seldom collected in flower but probably blooming chiefly in May.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Cordillera Central, El Tetero, *Ekman H13723* (S); Constanza, Gajo de la Angostura, *Ekman H14019a* (A, F, GH, K, NY, S, US); Constanza, behind Hotel Nueva Suiza, *Judd 1051* (A); Rancho del Medio, ca. 8 mi. S. of Loma del Oro, San José de las Matas, *Liogier 11568* (GH, NY); El Valle, headwater of Boa R., foot of La Pelona, *Liogier*

MAP 18. Distribution of *Lyonia tinensis* (dots) and *L. microcarpa* (circles).

12858 (NY); between Guácara and Guacarita rivers, La Guácara Arriba tributary to Bao R., *Liogier 13435* (F, IJ, NY, US); Loma la Sabrosa, S. of Rancho del Medio, Boa valley system, *Liogier 13490* (NY); Ciénaga de la Culata, Constanza, *Liogier 15984* (GH, NY, US).

Lyonia tinensis is closely related to *L. urbaniana* (see above for differences), *L. microcarpa,* and *L. truncata.* It can be readily distinguished from *L. microcarpa* by its leaves that are longer in relation to their width and that have brownish scales, and by its wider, five-merous capsules. *Lyonia tinensis* differs from *L. truncata* in its often more strongly toothed leaves with a densely raised-reticulate network of veins on the abaxial surface, its narrower capsules constricted at the apex, and its often smaller flowers. *Lyonia tinensis* is geographically isolated from *L. microcarpa* and *L. truncata* var. *truncata* since both of these taxa occur only in the Massif de la Selle–Sierra de Baoruco; it is isolated by habitat and elevational range from *L. urbaniana* and *L. truncata* var. *montecristina. Lyonia truncata* var. *montecristina* is found at elevations of ca. 100–1250 meters, while *L. tinensis* occurs at ca. 1100–1700 meters.

On a single plant the leaves can be acute to quite strongly truncate at the apex, or revolute to plane at the margin, and there is sometimes a marked variation in width or length of leaves between different individuals in the same population (see *Marcano 5761*). Occasionally plants have been found that are only very slightly pubescent on the abaxial leaf surface (e.g., *Judd 1051,* in part). Ultimate branchlets can be rigidly ascending to arching, depending on the vigor and habitat of the plant.

13. **Lyonia microcarpa** Urban & Ekman in Urban, Ark. Bot. **20A:** 36. 1926. TYPE: Haiti, Massif de la Selle, on the Morne Cabaio Road, [2200–2300 m. alt.], 24 August 1924, *E. L. Ekman H1609* (holotype, s!; isotypes, F!, GH!, IJ!, NY!, S!, US!).

Xolisma apiculata Sleumer, Repert. Sp. Nov. **36:** 270. 1934. *Lyonia apiculata* (Sleumer) Jiménez, Rhodora **62:** 237. 1960. TYPE: Dominican Republic, Cordillera de Bahoruco, prov. de Barahona [now Pedernales], Sierra del Comisario, 2100 m. alt., 30 August 1926, *E. L. Ekman H6813* (holotype, s!; isotype, IJ!).

Evergreen, usually low spreading shrub to ca. 2 meters tall (rarely small tree), with gray, longitudinally furrowed bark. Twigs slightly angled, slender, usually densely lepidote, otherwise glabrous. Buds ovoid, 1–2 by 0.7–1.4 mm. Leaf blades widely ovate or elliptic to nearly orbicular, 1–2.5(–3.5) by 0.8–2.5(–3) cm., ± flat, coriaceous, ca. 0.29–0.4 mm. thick; apex acute to truncate to rarely slightly acuminate; base cuneate to rounded or slightly cordate; margin plane to slightly revolute, distal portion strongly to obscurely and irregularly toothed (to rarely nearly entire), proximal portion obscurely toothed to entire; venation brochidodromous, 3° veins reticulate; adaxial surface often roughened due to thickened scale bases, lepidote but scales usually quickly deciduous, sparsely pubescent on proximal portion of midvein,

with 2° and 3° veins obscure, not depressed (less commonly with 2° veins slightly depressed); abaxial surface moderately to densely lepidote, otherwise densely pubescent, with all veins raised, forming dense and fine reticulum (often not visible without magnification); scales orange to orange-brown, persistent to less commonly deciduous, 0.12–0.34 mm. in diameter, usually erose; petiole 1–5 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 4- to 9-flowered. Pedicels clearly articulated with calyx, slender, 2–7 mm. long, lepidote, otherwise glabrous to very sparsely pubescent; bracteoles ± opposite, basal, narrowly triangular, 1–1.8 mm. long; bracts to ca. 2 mm. long. Flowers 4- or 5-merous; calyx lobes triangular, with acuminate apices, 0.8–1.3 by 0.4–0.8 mm., the adaxial side sparsely pubescent at margins and near apex, the abaxial side lepidote, otherwise glabrous; corolla cylindrical to long-urceolate, 3–4.5 by 1.8–2.5 mm., white, abaxially sparsely lepidote; filaments roughened, 1–2.7 mm. long, essentially unappendaged, anthers 0.6–1 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsules narrowly ovoid, (2.5–)3–4.5 by 1.5–2.5 mm., slightly lepidote, otherwise sparsely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.7–2.8 mm. long. (FIGURE 38.)

DISTRIBUTION AND ECOLOGY. Hispaniola, Massif de la Selle and Sierra de Baoruco (MAP 18). *Pinus occidentalis* forests and thickets, (1000–)1250–2300 m. alt. Near Aceitillar locally common in open pine forest on bright red, lateritic soil filling cavities of eroded limestone forming Sierra de Baoruco. Flowering probably chiefly May through July.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Sierra de Baoruco, Villa Aida, Aguacate, Loma del Toro, *Canela 54* (JBN); between Pedernales and Aceitial [Aceitillar], *Howard & Howard 8134* (GH, NY, S, US); near Aceitillar, *Judd 1463* (A); above Puerto Escondido, *Liogier 14060* (GH, NY, US); Loma del Toro, *Liogier 18168* (HJ, NY, US); between Las Mercedes and Aceitillar, Pedernales, *Liogier & Liogier 19661* (JBM, NY). **Haiti:** Morne des Commissaires, *Holdridge 933* (F, MO, NY, UC, US); dept. Ouest, Plateau Pistache, E. slope of Massif de la Selle, *Proctor 10752* (A, IJ, US).

Lyonia microcarpa is closely related to both *L. urbaniana* and *L. tinensis* but is easily recognized by its leaves with a very low length/width ratio, an often roughened adaxial surface, and densely packed, orange scales; its small corollas; and its small, narrowly ovoid, usually four-merous capsules. *Lyonia microcarpa* is geographically isolated from both of the above taxa (see MAPS 17 and 18) and is elevationally separated from the more distantly related *L. truncata* var. *truncata* (FIGURE 6). In the Sierra de Baoruco *L. microcarpa* usually occurs from 1250 to 2100 meters and *L. truncata* from (400 to) 900 to 1300 meters; in the Massif de la Selle (including Morne des Commissaires), *L. microcarpa* is found from 1600 to 2300 and *L. truncata* var. *truncata* from (600 to) 1000 to 1600 (to 1700) meters.

In the Sierra de Baoruco near Aceitillar, *Lyonia microcarpa* and *L. truncata* grow side by side and can be in flower at the same time, but no hybrids

between them have been seen. The flowers of *L. microcarpa* are about half the size of those of *L. truncata*, and differences in pollinators may help to isolate them. *Lyonia microcarpa* also seems to flower later: in early May, the plants near Aceitillar were just coming into flower, while *L. truncata* var. *truncata* was clearly past its peak of flowering and had many young fruits developing (pers. obs.). However, there is a single specimen (Haiti, Morne des Commissaires, ca. 1770 m., *Curtis s.n.*, 28 July 1944 (US)) that is intermediate between these two taxa and occurs at an elevation where both would be expected to grow; it may be a hybrid. Like *L. truncata*, it has larger, more elongate leaves with tertiary and higher order veins obscure on the abaxial surface, but it has the smaller, four-merous flowers and more densely lepidote leaves of *L. microcarpa*.

14. **Lyonia alpina** Urban & Ekman in Urban, Ark. Bot. **21A:** 53. 1927. TYPE: Haiti, Massif de la Selle, Morne de la Selle, in steep limestone side hills near the top (above Fonds Verettes), 2550–2650 m. alt., 1 February 1925, *E. L. Ekman H3162* (holotype, s!; isotypes, IJ!, K!, s!).

Xolisma orbiculata Sleumer, Repert. Sp. Nov. **36:** 272. 1934. *Lyonia orbiculata* (Sleumer) Jiménez, Rhodora **62:** 237. 1960. TYPE: Haiti, Massif de la Selle, Gauthier, high limestone ridge near Morne Courty, ca. 2600 m. alt., 20 February 1927, *E. L. Ekman H7624* (holotype, s!; isotypes, IJ!, s!, US!).

Evergreen, low, spreading shrub to ca. 0.5 meters tall, with gray, longitudinally furrowed bark. Twigs slightly angled, slender to stout, moderately lepidote, otherwise glabrous or very sparsely pubescent. Buds ovoid, 1–2 by 1–1.8 mm. Leaf blades ovate to broadly elliptic to orbicular, 1.1–3.1 by 0.9–2.6 cm., ± flat, coriaceous, ca. 0.5–0.6 mm. thick; apex truncate or rounded to nearly acute; base rounded to widely cuneate; margin plane to sometimes slightly revolute, distal portion obscurely and irregularly toothed, proximal portion toothed to entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely pubescent on proximal portion of midvein, veins obscure to sometimes faintly visible; abaxial surface moderately to densely lepidote, otherwise densely pubescent, with 2° and higher order veins usually obscure or nearly so, only very rarely raised and forming dense, fine reticulum; scales rust colored, persistent to deciduous, ca. 0.08–0.2 mm. in diameter, usually ± erose; petiole 3–5 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 5- to 8-flowered. Pedicels clearly articulated with calyx, slender, 2–6 mm. long, lepidote, otherwise glabrous or vary sparsely pubescent; bracteoles ± opposite, basal, narrowly triangular, 1.5–2 mm. long; bracts to ca. 2.5 mm. long. Flowers 4- or 5-merous; calyx lobes triangular, with acuminate apices, 1.5–2 by 0.7–1.4 mm., the adaxial side pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous; corolla cylindrical, 5–6.5 by 3–4 mm., white, abaxially sparsely lepidote; filaments roughened, ca.

3.5 mm. long, essentially unappendaged, anthers ca. 1.3 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ± globose to short-ovoid, 3–4 by 3–4 mm., slightly lepidote, otherwise sparsely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.4–2 mm. long. (FIGURE 40.)

DISTRIBUTION AND ECOLOGY. Haiti, Massif de la Selle (MAP 17). Limestone ridges, ca. 2550–2650 m. alt.

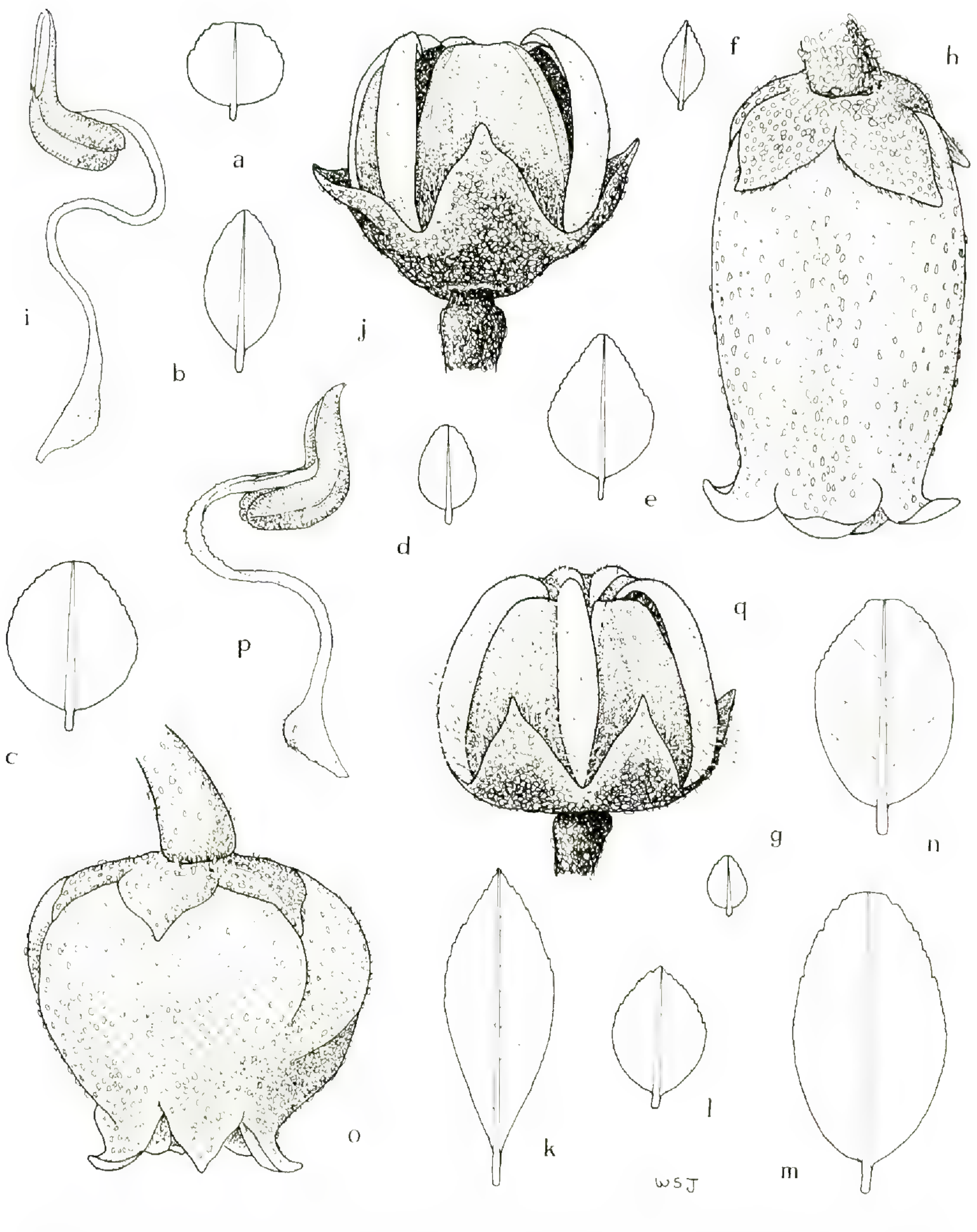


FIGURE 40. a–j, *Lyonia alpina:* a–g, leaves, × .5; h, flower, × 6; i, stamen, × 12.5; j, capsule, × 6. k–q, *L. alainii:* k–n, leaves, × .5; o, flower, × 6; p, stamen, × 12.5; q, capsule, × 6.

REPRESENTATIVE SPECIMENS. Known only from the type collections.

Lyonia alpina has been poorly collected, and its relationships are still somewhat obscure. It is probably close to *L. truncata* var. *truncata* since the two have similarly shaped leaves with densely pubescent, obscurely veined abaxial surfaces and more or less smooth adaxial surfaces; large, more or less cylindrical corollas; and wide capsules. *Lyonia alpina* can be distinguished by its shorter, four- or five-merous capsules, and its more coriaceous, more densely lepidote leaves. *Lyonia alpina* is also possibly related to *L. microcarpa*, as indicated by its often four-merous flowers, its small, often densely ferrugineous leaves, and its low, spreading habit. It is of interest that the venation is very rarely slightly raised-reticulate on the abaxial leaf surface, a character typical of *L. microcarpa*, although the one twig (see *Ekman H3162* (s, in part)) that shows this condition also has quite narrow capsules and could possibly represent a hybrid between *L. alpina* and *L. microcarpa*. *Lyonia alpina* can easily by differentiated from *L. microcarpa* by the shape and size of its capsules, its long calyx lobes and corollas, the obscure venation of its abaxial leaf surface (vs. raised-reticulate in *L. microcarpa*), and its smooth adaxial epidermis (vs. often roughened in *L. microcarpa*). *Lyonia alpina* occurs at elevations higher than those of any other species of the genus in the Massif de la Selle (see FIGURE 6) and is isolated altitudinally from both *L. truncata* var. *truncata* and *L. microcarpa*.

Lyonia orbiculata (based on *Ekman H7624*, in flower) differs from the type of the earlier-described *L. alpina* (*Ekman H3162*, in fruit) only in its slightly larger, more nearly orbicular, and more often truncate leaves; a note by Ekman on the holotype of *L. orbiculata* reads: "same as no. *3162*, now in flower." Thus Ekman, the only botanist to have seen this taxon in the field, considered his *7624* to be the same species as his earlier collection and was collecting it to complement the earlier one. Ekman's judgment is correct. Similar variation in leaf shape and apex type is common in *L. truncata*, *L. microcarpa*, *L. urbaniana*, and *L. tinensis*.

15. **Lyonia truncata** Urban, Symb. Antill. **7:** 318. 1912.

Evergreen, low to erect, often densely branched shrub to medium-sized tree to 2.5–7 meters tall, with gray to brownish, longitudinally furrowed bark. Twigs slightly to moderately angled, slender, sparsely lepidote, otherwise usually sparsely pubescent. Buds ovoid, 0.7–1.7 by 0.7–1.1 mm. Leaf blades elliptic to ovate or occasionally obovate, 0.8–5(–6.8) by 0.4–2(–3) cm., ± flat to recurved or slightly concave, coriaceous, ca. 0.2–0.4 mm. thick; apex acute to rounded or truncate (rarely slightly acuminate); base rounded to narrowly cuneate; margin plane to slightly revolute toward petiole, distal portion clearly to obscurely and irregularly toothed to entire, proximal portion undulate or entire to obscurely and irregularly toothed; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely to moderately pubescent on proximal portion of midvein, with veins obscure to faintly visible and reticulate, not depressed (occasionally

with midvein and/or few 2° veins slightly depressed); abaxial surface moderately lepidote, otherwise densely (rarely only sparsely) pubescent, the 3° and higher order veins ± flat, obscure to occasionally slightly and laxly reticulate, the 2° veins obscure to very occasionally slightly raised and visible; scales rust colored but becoming whitish with age, usually persistent, ca. 0.08–0.2 mm. in diameter, erose to entire; petiole 1–7.5 mm. long, lepidote, otherwise pubescent adaxially. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 4- to 11-flowered. Pedicels clearly articulated with calyx, slender, 2.5–10(–13) mm. long, lepidote, otherwise glabrous to moderately pubescent; bracteoles ± opposite, basal, narrowly triangular, ca. 0.7–1 mm. long; bracts to ca. 1.5 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate to occasionally acute apices, 1–2 by 0.5–1.1 mm., the adaxial side slightly pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous; corolla cylindrical, 4–7 by 2–3.5(–4) mm., white or sometimes slightly pink tinged, abaxially sparsely lepidote; filaments roughened, 3–4 mm. long, unappendaged, anthers 1–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to ellipsoid, (3–)4–6.5 by (2.5–)3–4.5(–5) mm., slightly lepidote, otherwise sparsely to moderately pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–3 mm. long.

DISTRIBUTION. Hispaniola; low-elevation pine forests and thickets of Massif de la Selle, Massif du Nord, Sierra de Baoruco, and Cordillera Central; 100–1600(–1700) m. alt.

Key to the Varieties of *Lyonia truncata*

1. Leaves 0.8–3.5(–4) cm. long, held erectly, slightly concave to lax and ± flat, sometimes slightly recurved; shrub to 2.5(–3) m. tall, often densely branched; [Sierra de Baoruco and Massif de la Selle, ca. 400–1700 m. alt.] . . . . . 15a. var. *truncata*.
1. Leaves (2.5–)3–5(–6.8) cm. long, held more laxly, ± flat to recurved; shrub to small tree to 3–7 m. tall, branching more open; [Cordillera Central and Massif du Nord, ca. 100–1250 m. alt.] . . . .15b. var. *montecristina*.

15a. **Lyonia truncata** Urban var. **truncata**

Xolisma truncata (Urban) Small, N. Am. Fl. **29**(1): 70. 1914. TYPE: Dominican Republic, prov. Barahona [Pedernales], ad Arroyo seco, 400 m. alt., April 1912, *Fuertes 1528* (holotype, B (destroyed); fragment of holotype, NY!; isotypes, F!, GH!, K!, L!, NY (2 sheets)!, P!, US (2 sheets)!, W!).

Lyonia tippenhaueri Urban, Symb. Antill. **8:** 515. 1920. TYPE: Haiti, Port-au-Prince, Thebaud, Auslauf des Morne Brouet, 1600 m. alt., September 1919, *W. Buch 1716* (holotype, B (destroyed); isotypes, GH!, IJ!).

Lyonia haitiensis Urban, Symb. Antill. **8:** 514. 1920. TYPE: Haiti, Port-au-Prince, Camp franc, 1800 m. [actually 1500 m.] alt., August 1917, *W. Buch 1408* (holotype, B (destroyed); isotypes, GH!, IJ!).

Lyonia furcyensis Urban, Repert. Sp. Nov. **18:** 193. 1922. TYPE: Haiti,

vicinity of Furcy, 1300 m. alt., 26 May–15 June 1920, *E. L. Leonard 4742* (holotype, B (destroyed); isotypes, NY!, US!).

Lyonia brachycarpa Urban & Ekman in Urban, Ark. Bot. **20A:** 34. 1926. TYPE: Haiti, Massif de la Selle, ridge between Morne Tranchant and Morne Brouet, 1500–1600 m. alt., 27 July 1924, *E. L. Ekman H1151* (holotype, s!; isotypes, s!, US (2 sheets)!).

Lyonia plumeri Urban & Ekman in Urban, Ark. Bot. **21A:** 53. 1927. TYPE:

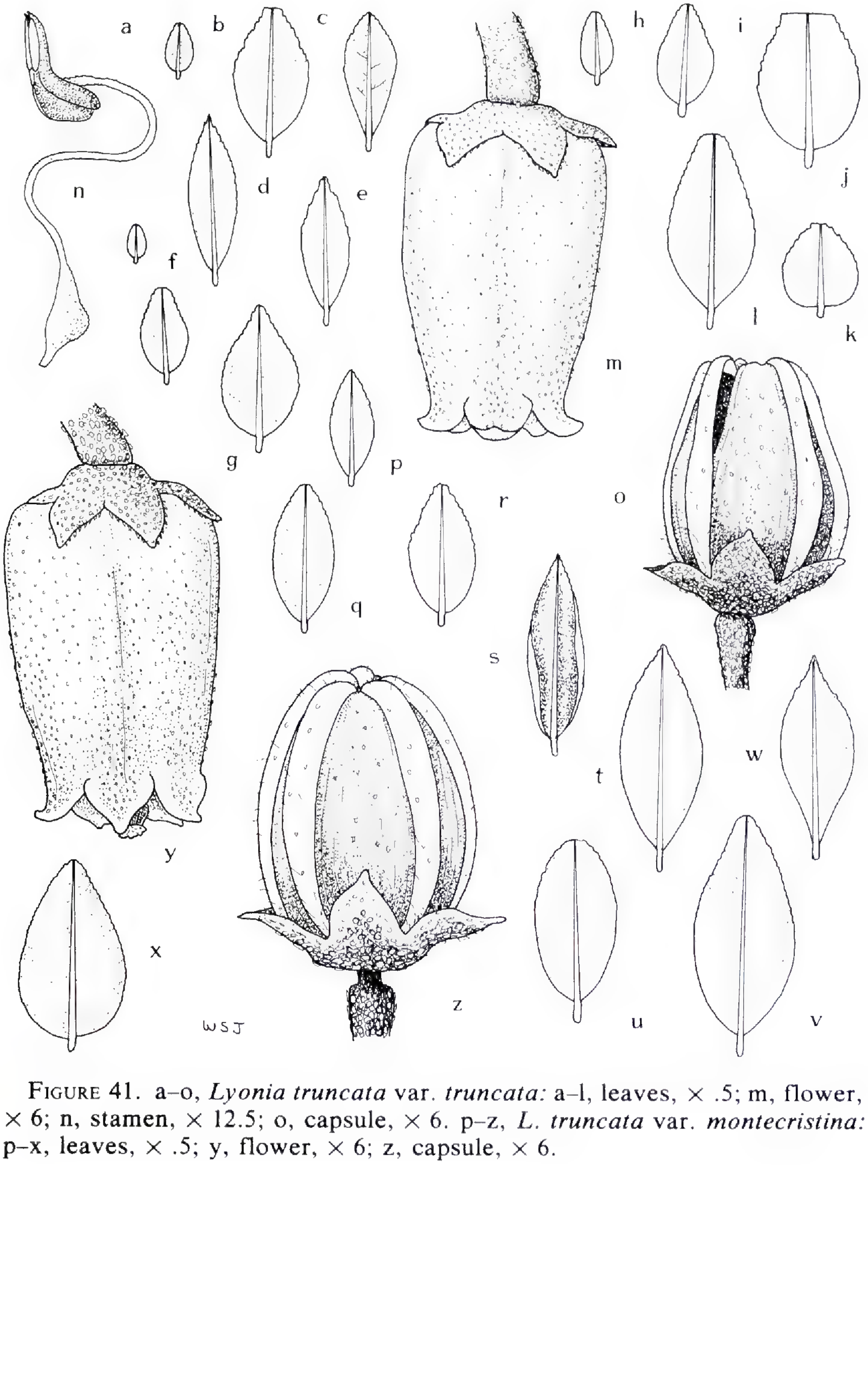
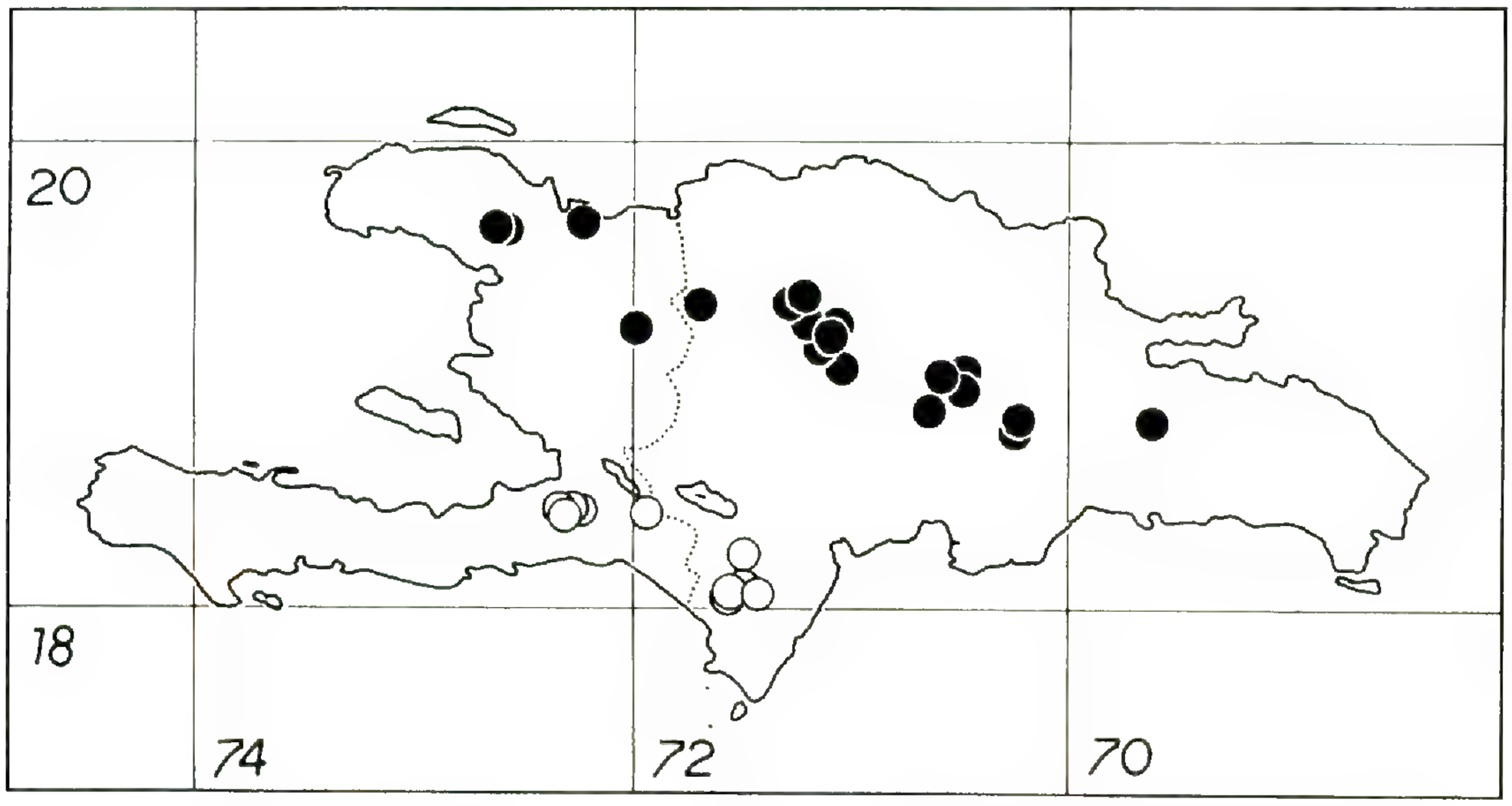


FIGURE 41. a–o, *Lyonia truncata* var. *truncata:* a–l, leaves, × .5; m, flower, × 6; n, stamen, × 12.5; o, capsule, × 6. p–z, *L. truncata* var. *montecristina:* p–x, leaves, × .5; y, flower, × 6; z, capsule, × 6.



MAP 19. Distribution of *Lyonia truncata* var. *truncata* (circles) and *L. truncata* var. *montecristina* (dots).

Haiti, Massif de la Selle, group Crête-à-Piquants, Port-au-Prince, near Desroziers, 1100 m. alt., 19 April 1926, *E. L. Ekman H5881* (holotype, S!; isotypes, NY!, S!, US (2 sheets)!).

Evergreen, low to erect, often densely branched shrub to 2.5(–3) meters tall, with branches often rigidly ascending; internodes near midpoint of branches of previous year 0.2–1.2 cm. long (avg. 0.6–0.7), slightly longer in rapidly growing branches. Leaf blades 0.8–3.5(–4) by 0.4–2(–3) cm., slightly concave to ± flat, sometimes slightly recurved; margin plane with distal portion obscurely and irregularly toothed to clearly toothed or notched; petiole 1–5 mm. long. Pedicels 2.5–10(–13) mm. long. (FIGURES 41, 42.)

DISTRIBUTION AND ECOLOGY. Hispaniola, Massif de la Selle and Sierra de Baoruco (MAP 19). *Pinus occidentalis* forests and thickets, (400–)900–1600(–1700) m. alt. Commonly on red lateritic soils with *Andropogon urbanianus* and shrubs such as *Garrya fadyenii, Citharexylum schulzii, Coreopsis buchii, Bumelia repens, Heterotrichum angustifolium, Senecio picardae, Narvalina domingensis, Eupatorium illitum*, and *Hypericum hypericoides*. Flowering chiefly late February to June.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Sierra de Baoruco, Rancho Viejo, S. of Puerto Escondido, *Howard 12153* (A, US); Aceitillar No. 1, *Jiménez*

FIGURE 42. a, *L. truncata* var. *montecristina:* note lax branches with more elongated leaves (leaf blade often curved toward abaxial surface); photo taken in Cordillera Central, near La Diferencia, ca. 640 meters alt. b, *Lyonia truncata* var. *truncata:* note rigidly ascending branches with small, rounded leaves (leaf blade not curved toward abaxial surface); photo taken in Sierra de Baoruco, near Aceitillar, 1000 meters alt.

b
a

3270 (HJ, US, USD); S. of Aceitillar, *Judd 1466* (A); Hoyo de Pelempito, *Liogier 18134* (HJ, NY, US); Las Mercedes and Aceitillar, *Liogier & Liogier 19661a* (NY); Cayo, Aceitillar, *Liogier & Liogier 19642* (HJ, JMB, NY). **Haiti:** Massif de la Selle, Morne Brouet, Port-au-Prince, *Buch 1939* (GH, IJ); Morne Tranchant, *Ekman H1247* (A, F, S); Nouvelle Touraine on ridge above Chapelle Taure, *Ekman H1376* (NY, S); Crête-à-Piquants, Port-au-Prince, Morne Desroziers, *Ekman H7398* (A, F, IJ, S); Croix-des-Bouquets, Bodeau, *Ekman H7868* (S); Pétionville, Furcy, *Ekman H8022* (A, F, IJ, S, US); trail to DuBois, N. of Fond Verrettes, *Holdridge 1389* (GH, NY, US).

15b. **Lyonia truncata** Urban var. **montecristina** (Urban & Ekman) Judd, comb. et stat. nov.

Lyonia montecristina Urban & Ekman in Urban, Ark. Bot. **24A:** 33. 1932. *Xolisma elongata* Sleumer, Repert. Sp. Nov. **36:** 271. 1934. *Lyonia elongata* (Sleumer) Jiménez, Rhodora **62:** 237. 1960. TYPE: Dominican Republic, Cordillera Central, prov. de Monti Cristi [Dajabon], N. of Restauración, ca. 700 m. alt., 4 June 1926, *E. L. Ekman H6249* (holotype, s!; isotypes, IJ!, NY!, US!).

Evergreen, erect shrub to medium-sized tree to 3–7 meters tall, with branching open and lax to rigidly ascending in vigorous young shoots; internodes near midpoint of branches of previous year 0.5–1.8 cm. long (avg. 0.8–0.9), longer in rapidly growing branches. Leaf blades (2.5–)3–5(–6.8) by 0.7–2(–3) cm., ± flat to recurved; margin plane to slightly revolute toward petiole, distal portion obscurely and irregularly toothed to undulate or entire; petiole 2–7.5 mm. long. Pedicels 3–8 mm. long. (FIGURES 41, 42, 44.)

DISTRIBUTION AND ECOLOGY. Dominican Republic and Haiti, Massif du Nord and Cordillera Central (MAP 19). Low-elevation *Pinus occidentalis* forests and thickets, 100–1200 m. alt. Flowering chiefly March through May.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Cordillera Central, near Jarabacoa, *Bro. Augusto 893* (NY); Bayaguana, slope of Loma Manaquá, *Ekman H11102* (GH, NY, S, US); Salto de Constanza, *Jiménez 2207* (HJ, US, USD); Antonsape El Bueno, San José de las Matas, *Jiménez et al. 5571* (HJ, NY); La Cidra, *Jiménez et al. 2900* (HJ, US, USD); S. of El Rubio, *Judd 1339* (A); between El Rubio and La Diferencia, *Judd 1342* (A); near Dajao R., La Diferencia, *Liogier 11292* (GH, IJ, JBM, NY); La Manaclita, above Alarrobos, ca. 8 mi. S. of La Vega, *Liogier 11456* (GH, IJ, NY); between Mata Grande and Antonzapa rivers, *Liogier 12989* (GH, IJ, NY); Barrancón, from Bonao to Hato Viejo, *Liogier 14852* (NY); Loma Peguera, Bonao, *Liogier 18552* (HJ, NY, US); between Monción and La Leonor, *Liogier & Liogier 22600* (JMB); Arroyo Jicomé, distr. San José de las Matas, *Valeur 624* (F, IJ, MO, NY, US). **Haiti:** Massif du Nord, Morne Haut-du-Cap, in Morne Bois-Pin, *Ekman H2893* (IJ, S, US); Gros-Morne, Morne Belanse, spur toward La Brande, *Ekman H3902* (GH, IJ, S, US); Hinche, at Bois-Charles, *Ekman H6076* (IJ, NY, S); La Brande to Mt. Balance, *Nash & Taylor 1669* (NY).

Lyonia truncata is closely related to *L. rubiginosa*, *L. tinensis*, and *L. alpina;* it differs from *L. rubiginosa* vars. *costata* and *stahlii* in having leaves

with the secondary veins obscure to visible but usually not depressed on the adaxial surface, and with a dense covering of unicellular hairs on the abaxial surface. It can be distinguished from *L. rubiginosa* var. *rubiginosa* by its usually truncate to rounded or acute (not acuminate) leaf apices, its more obscure venation on the abaxial leaf surfaces, and its narrower capsules. It differs from *L. tinensis* in its often more obscurely toothed leaves that lack a dense and fine, raised, reticulate network of veins on the abaxial surface, its wider capsules without constricted apices, and its often larger flowers. Finally, *L. truncata* can easily be distinguished from *L. alpina* by its habit, its longer and more consistently five-merous capsules, and its less coriaceous and less lepidote leaves. *Lyonia truncata* var. *truncata* differs from var. *montecristina* in its habit and its smaller, more erectly held leaves (FIGURE 42); the two varieties are geographically isolated (MAP 19). *Lyonia truncata* is geographically isolated from *L. rubiginosa* vars. *rubiginosa* and *stahlii*, since these taxa do not occur on Hispaniola. It is altitudinally isolated from *L. alpina*, *L. tinensis*, and *L. rubiginosa* var. *costata* (see FIGURES 4–6). This species is also altitudinally isolated from *L. microcarpa*, although rare hybrids may occur between them.

A few specimens (e.g., *Buch 1716* (type of *L. tippenhaueri* Urban) and *Ekman H1247*, from the zone of overlap between *Lyonia truncata* var. *truncata* and *L. rubiginosa* var. *costata* in the Massif de la Selle) have leaves that have more prominent secondary veins and that are only sparsely covered with unicellular hairs on the abaxial surface; these might represent hybrids. However, the author has not been able to collect on the Massif de la Selle, and in the Sierra de Baoruco occasional plants that otherwise have the usual characters of *L. truncata* var. *truncata* are only sparsely pubescent.

Lyonia truncata vars. *truncata* and *montecristina* are probably best kept together in one rather variable species for several reasons. First, although populations in the Cordillera Central and the Sierra de Baoruco of the Dominican Republic seem very distinct, as one moves westward in each of these mountain ranges the differences become less marked; the populations of the Massif du Nord and the Massif de la Selle of Haiti are much less distinctive and are clearly very closely related. Second, the differences between the two taxa are based solely on plant habit and leaf size, while most species of sect. LYONIA have distinctive flowers and/or fruits in addition to vegetative differences. Finally, differences such as leaf shape and size have proved to be quite plastic in this group of West Indian species and must be used with care in separating taxa.

Seedlings and very young shrubs are common in open areas and characteristically have smaller and narrower leaves with fewer unicellular hairs and more acute apices than do mature plants. Young shrubs frequently form a woody burl that repeatedly sends up shoots; young shoots are densely ferrugineous and are often reddish. Leaves of vigorously growing shoots are sometimes acute or even slightly acuminate with strongly toothed margins, and unicellular hairs may be nearly lacking below. There is much variation in the shape and size of leaves, leaf apices, and marginal dentation, even within a single population. Occasional plants with only a few unicellular

hairs on the abaxial leaf surfaces have been found; these always occur in populations of "normal" densely pubescent plants and are perfectly characteristic of *Lyonia truncata* in all other features. These plants are not hybrids with species of *Lyonia* lacking unicellular hairs on the lower leaf surfaces (e.g., *L. rubiginosa, L. tuerckheimii, L. alainii*) but are merely one extreme in the range of variation of this character in the taxon. As small trees, many plants have a columnar habit that is quite reminiscent of that of *L. jamaicensis* or some plants of *L. rubiginosa*.

16. **Lyonia alainii** Judd, sp. nov.

Frutices sempervirentes ad 2.5 m. alti, cortice ravida longistrorsum sulcata. Ramuli hornotini moderate angulati, graciles, lepidoti, interdum leviter pubescenti. Folia subobovata-elliptica vel fere orbiculata, 2.3–6(–8) cm. longa, 1–3(–5) cm. lata, coriacea; ad apicem acuta, obtusa, rotundata vel truncata; ad basin cuneata vel rotundata; margo planiuscula vel subrevoluta, in parte distali plerumque subdentata, in parte proximali integra vel subintegra; nervus primarius prominens; nervi secundarii obscuri vel interdum depressi; pagina abaxialis lepidota non pilifera; petioli 2–9 mm. longi. Inflorescentiae fasciculatae, cum ca. 4 ad 12 floribus. Pedicelli graciles cum calyce articulati, 6–15 mm. longi. Flos plerumque 5-merus. Calyx lobis 1–2 mm. longis, 1–2 mm. latis. Corolla urceolata, 3.5–4.5 mm. longa, 3.5–4.5 mm. lata, alba, sparsim lepidota in pagina abaxiali. Filamenta 2–2.5 mm. longa, haud calcarata; antherae 1–1.2 mm. longae. Capsula ± globosa, vel brevissime ovoidea, 3–4.5 mm. longa, 4–5 mm. lata, pilis unicellularibus moderate vel dense vestita, suturis pallentibus et incrassatis.

Evergreen shrub to ca. 2.5 meters tall, with grayish, longitudinally furrowed bark. Twigs moderately angled, slender, sparsely lepidote, otherwise glabrous to sparsely pubescent. Buds ovoid, 1–2 by 0.8–1.5 mm. Leaf blades elliptic to slightly obovate, or nearly orbicular, 2.3–6(–8) by 1–3(–5) cm., ± flat to slightly recurved, quite coriaceous, ca. 0.33–0.43 mm. thick; apex acute to rounded or truncate; base narrowly cuneate to rounded; margin plane to slightly revolute, distal portion ± obscurely and irregularly toothed (to occasionally clearly and irregularly toothed), proximal portion entire or nearly so; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely pubescent on proximal portion of midvein, 3° veins obscure to slightly visible, 2° veins sometimes depressed; abaxial surface moderately lepidote, otherwise glabrous, the 3° and higher order veins obscure to very slightly raised but not forming dense, fine, raised network, the 2° veins usually at least slightly raised and clearly visible; scales rust colored but becoming whitish with age, persistent to deciduous, ca. 0.07–0.14 mm. in diameter, entire to erose; petiole 2–9 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 4- to 12-flowered. Pedicels clearly articulated with calyx, slender, 6–15 mm. long, lepidote, otherwise sparsely pubescent; bracteoles ± opposite, basal, narrowly triangular, 0.8–1.5 mm.

long; bracts to ca. 1.3 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 1–2 by 1–2 mm., the adaxial surface sparsely pubescent especially near apex, the abaxial surface lepidote, otherwise glabrous to sparsely pubescent; corolla urceolate, 3.5–4.5 by 3.5–4.5 mm., white or sometimes pink tinged, abaxially sparsely lepidote; filaments roughened, 2–2.5 mm. long, essentially unappendaged, anthers 1–1.2 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ± globose or very short-ovoid, 3–4.5 by 4–5 mm., slightly lepidote, otherwise moderately to densely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.3–2 mm. long. (FIGURE 40.)

TYPE: Dominican Republic, Loma La Sabrosa, 1500 m. alt., S. of Rancho del Medio Mata Grande, San José de las Matas, 5–9 November 1968, *Liogier 13476* (holotype, NY!; isotype, US!).

DISTRIBUTION AND ECOLOGY. Dominican Republic (MAP 17). Known only from Loma la Sabrosa (in thickets in *Pinus occidentalis* forest) and Loma de la Sal (in moist cloud forest) in the Cordillera Central; ca. 1300–1500 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Dominican Republic:** Loma de la Sal, Jarabacoa, *Liogier 13344* (GH, NY), *13377* (GH, NY), *13379* (GH, IJ, NY).

Lyonia alainii is most closely related to *L. rubiginosa* var. *costata* and *L. tuerckheimii*. It differs from both in its small, urceolate flowers, its subglobose to very short-ovoid and often densely pubescent capsules, and its more obscurely toothed leaves. In addition, *L. alainii* can be distinguished from *L. tuerckheimii* by its more slender twigs with only a few unicellular hairs, and from *L. rubiginosa* var. *costata* by its more coriaceous leaves with more strongly lignified (and thickened) inner periclinal walls of the adaxial epidermis. Sterile specimens will probably be most easily confused with *L. rubiginosa* var. *costata*. *Lyonia alainii* is geographically isolated from both of the above taxa since neither occurs in the Loma de la Sal or the Loma la Sabrosa; it is also altitudinally isolated from *L. tuerckheimii* (see FIGURE 5).

I am pleased to be able to name this distinctive species after Dr. Alain H. Liogier, who has collected extensively throughout the Dominican Republic, Cuba, and Puerto Rico. Without his collections, made in various seasons and often from quite inaccessible localities, it would have been difficult or impossible to accomplish a satisfactory revision of *Lyonia*.

17. **Lyonia tuerckheimii** Urban, Symb. Antill. **7:** 317. 1912.

Xolisma tuerckheimii (Urban) Small, N. Am. Fl. **29**(1): 71. 1914. TYPE: Dominican Republic, near Constanza, in Valle Nuevo, 2200 m. alt., April 1910, *von Tuerckheim 3154* (holotype, B (destroyed); isotypes, M!, NY!, US!, W!).

Lyonia eggersii Urban, Symb. Antill. **7:** 534. 1913. *Xolisma eggersii* (Urban) Small, N. Am. Fl. **29**(1): 71. 1914. TYPE: Dominican Republic, near

Constanza, in Valle Nuevo, 2270 m. alt., 29 May 1887, *Eggers 2199*[b] (holotype, B (destroyed); fragment of holotype, NY!).

Evergreen, usually compact shrub to 2(–2.5) meters tall, often from an underground woody burl, with gray, longitudinally furrowed bark. Twigs slightly to moderately angled, stout, sparsely to moderately lepidote, otherwise usually densely pubescent. Buds ovoid, 0.7–2 by 0.9–2 mm., lepidote. Leaf blades elliptic to ovate (less commonly obovate), 1.8–5(–6.5) by 0.8–2.5(–3.6) cm., ± flat, strongly coriaceous, ca. 0.35–0.47 mm. thick; apex acute, rounded, or truncate; base narrowly cuneate to rounded; margin plane (less commonly very slightly revolute), distal portion strongly to obscurely and irregularly toothed, proximal portion entire to obscurely toothed; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, densely pubescent on midvein, sometimes sparsely pubescent on major 2° veins, the veins faintly visible to obscure, occasionally some 2° veins very slightly depressed; abaxial surface moderately lepidote, otherwise glabrous, but often sparsely to moderately pubescent on midvein, especially proximal portion, the 3° and higher order veins obscure to very slightly raised, not forming dense, fine, raised network, the 2° veins obscure to slightly raised and visible; scales rust colored, persistent to deciduous, ca. 0.08–0.25 mm. in diameter, erose to nearly entire; petiole 2.6–6(–8) mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate (to rarely shortly racemose), 5- to 18-flowered. Pedicels clearly articulated with calyx, slender, 4–13(–17) mm. long, lepidote, otherwise usually densely pubescent; bracteoles opposite to subopposite, basal or nearly so, narrowly triangular, 1.3–2 mm. long; bracts to ca. 3 mm. long. Flowers 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 1.2–2 by 0.8–1.4 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous to sparsely pubescent (near base); corolla cylindrical, (5.5–)6.5–10 by (2.4–)3–4.5 mm., white, usually slightly pink tinged especially near mouth, abaxially sparsely lepidote; filaments roughened, 3–5.5 mm. long, unappendaged (or occasionally with very minute spurs near junction with anthers), anthers 1–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ellipsoid to ovoid, 4–7 by 3–5 mm., slightly lepidote, otherwise sparsely to densely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.2–2.5 mm. long. (FIGURES 43, 44.)

DISTRIBUTION AND ECOLOGY. Hispaniola (MAP 20). Chiefly in high-elevation *Pinus occidentalis* forests of the Cordillera Central, (1700–)2000–3100 m. alt.; a single collection known from Massif de la Selle, 2500 m. alt. Sprouting frequently from base of plant after fires. Flowering probably chiefly late March through June.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Cordillera Central, Sierra de Ocoa, San José de Ocoa, Cuchilla del Pino Atravesado, *Ekman H11707* (A, F, GH, K, NY, S, US); San Juan, Lomas de la Mediania, *Ekman H13549* (S, US); Valle Nuevo toward Sabana Alta, *Ekman H13785* (S, US); Valle Nuevo, near "the moment," *Judd 1138* (A); between Constanza and Valle Nuevo,

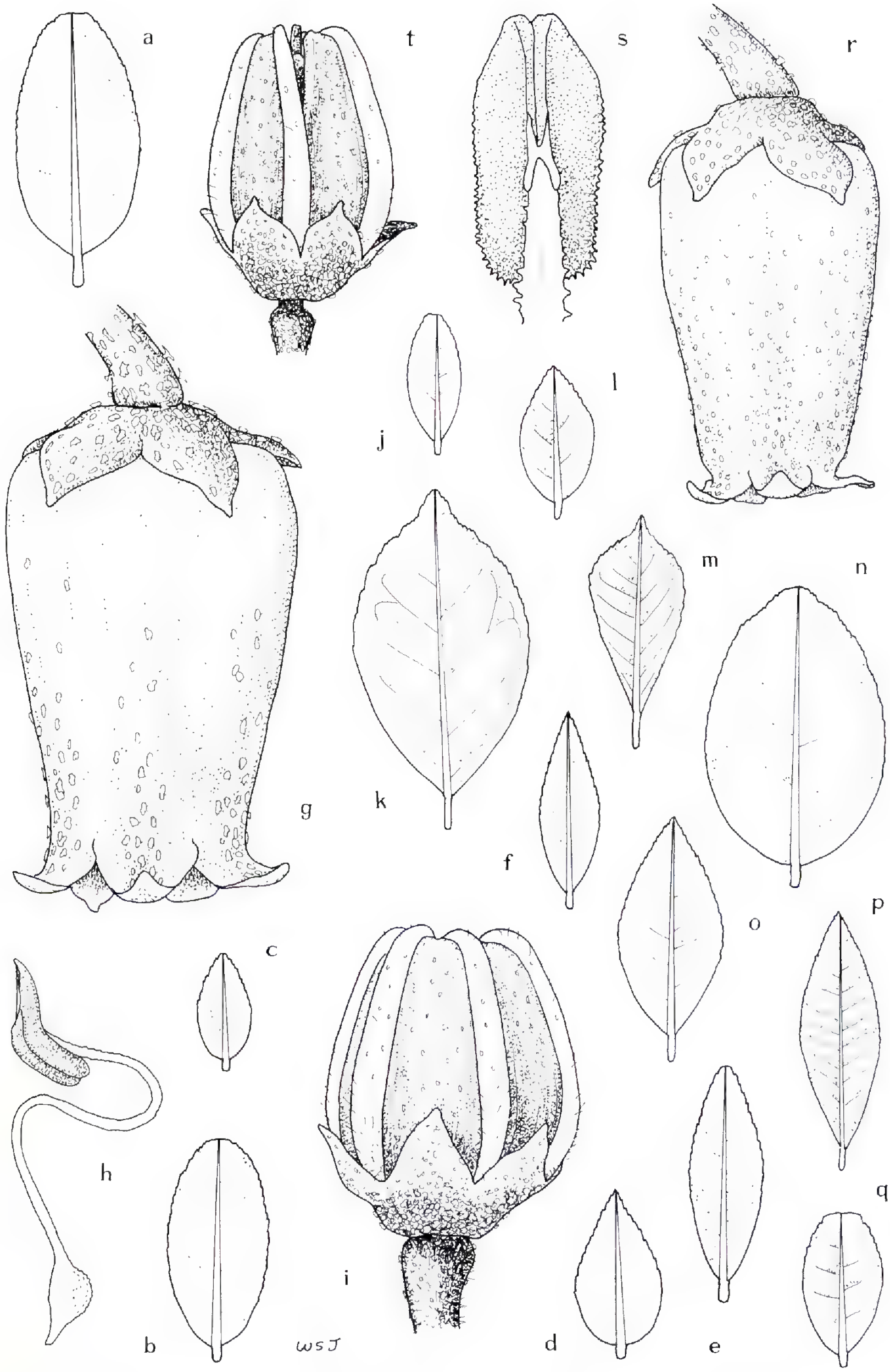


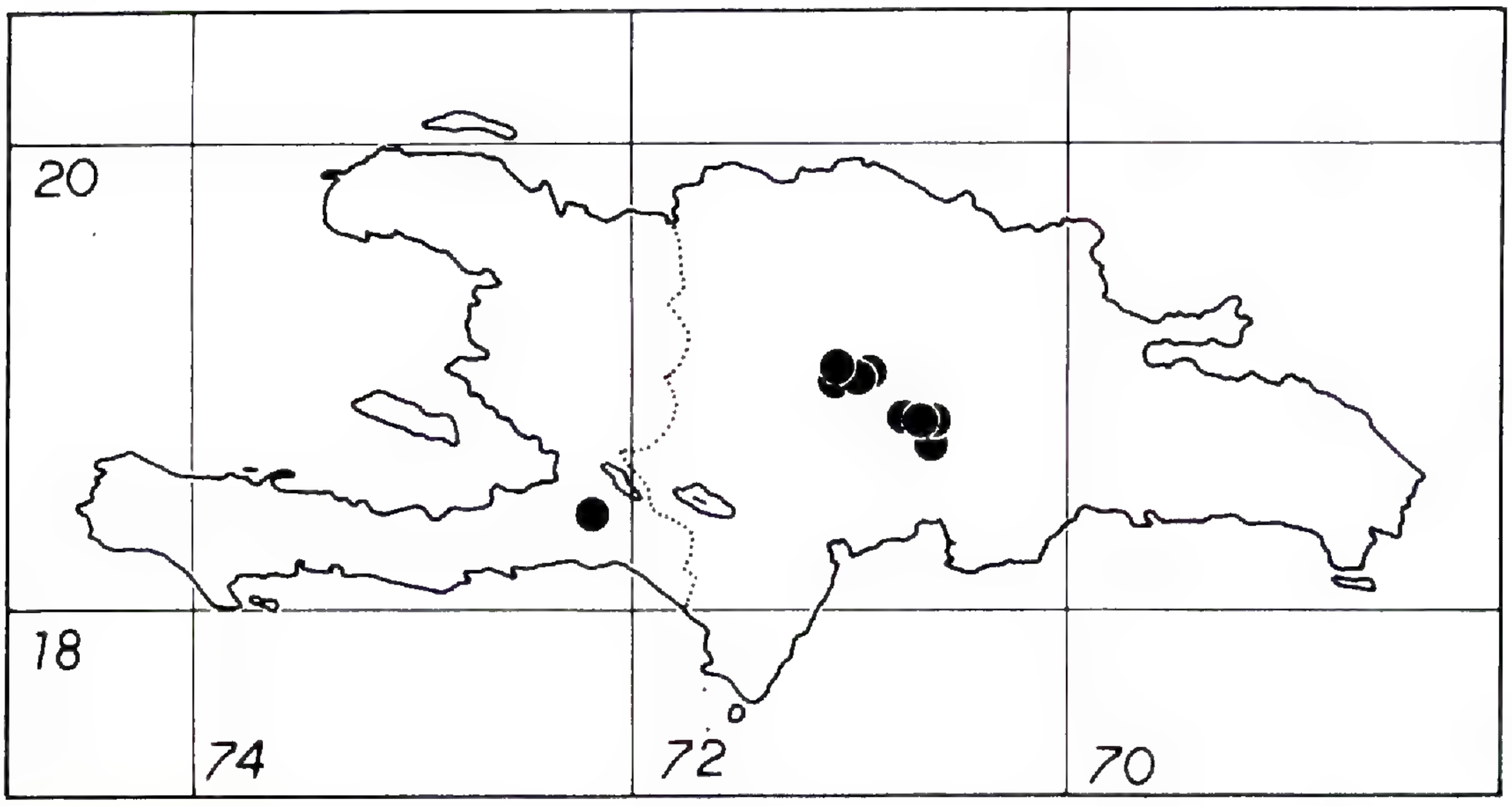
FIGURE 43. a–i, *Lyonia tuerckheimii:* a–f, leaves, × .5; g, flower, × 6; h, stamen, × 12.5; i, capsule, × 6. j–t, *L. rubiginosa* var. *costata:* j–q, leaves, × .5; r, flower, × 6; s, anther, × 25; t, capsule, × 6.

a

b

d

c



MAP 20. Distribution of *Lyonia tuerckheimii*.

Judd 1198 (A); between La Nuez and "the monument," *Judd 1222* (A); upper Bao valley, at foot of La Pelona, *Liogier 12910* (GH, NY); Ciénaga de Manabao, Jarabacoa, *Liogier 17195* (US); La Rucilla, *Liogier 17197* (NY, US); La Cotorra, *Marcano s.n.*, 10 April 1964 (USD); Pico Duarte, *Marcano* [Herb. Jiménez No.] *4944* (HJ, US, USD); El Pico del Yaque [= La Rucilla], *Mera & Jiménez* [Herb. Jiménez No.] *233* (HJ, US). **Haiti:** Massif de la Selle, Croix-des-Bouquets, high ridges toward Morne Mérillon, *Ekman H7625* (GH, IJ, NY, S).

Lyonia tuerckheimii, a quite distinctive species, can be easily differentiated from its relatives *L. alainii* and *L. rubiginosa* var. *costata* by its much thicker and more robust branches that are densely covered with unicellular hairs and by the adaxial hypodermis of its leaves, which is two cells thick. In addition, it differs from *L. alainii* in its cylindrical corollas and its ellipsoid to ovoid, often more sparsely pubescent capsules, and from *L. rubiginosa* var. *costata* in its more coriaceous leaves with secondary veins usually not depressed, its habit, and its more robust capsules (FIGURE 45). *Lyonia tuerckheimii* is isolated from both of the above taxa by habitat (and thus altitudinal) differences (FIGURES 5, 6); it occurs chiefly in the high-elevation

FIGURE 44. a, *Lyonia truncata* var. *montecristina* (*Liogier 11456*, NY): leaves with secondary and higher order veins obscure on abaxial surface; note also leaves with dense layer of unicellular hairs on abaxial surface and apices varying from acute to truncate even in single specimen. b, *L. tuerckheimii* (*Ekman 13785*, S): note stem covered with small, unicellular hairs; leaves lacking unicellular hairs on abaxial surfaces and with secondary veins not depressed. c, *L. rubiginosa* var. *costata* (*Liogier 13075*, GH): note more slender twig; secondary veins slightly depressed. d, *L. nipensis* var. *nipensis* (*Ekman 18153*, S): note leaf margins not or only slightly revolute and secondary veins not depressed. Scale = 2 cm.

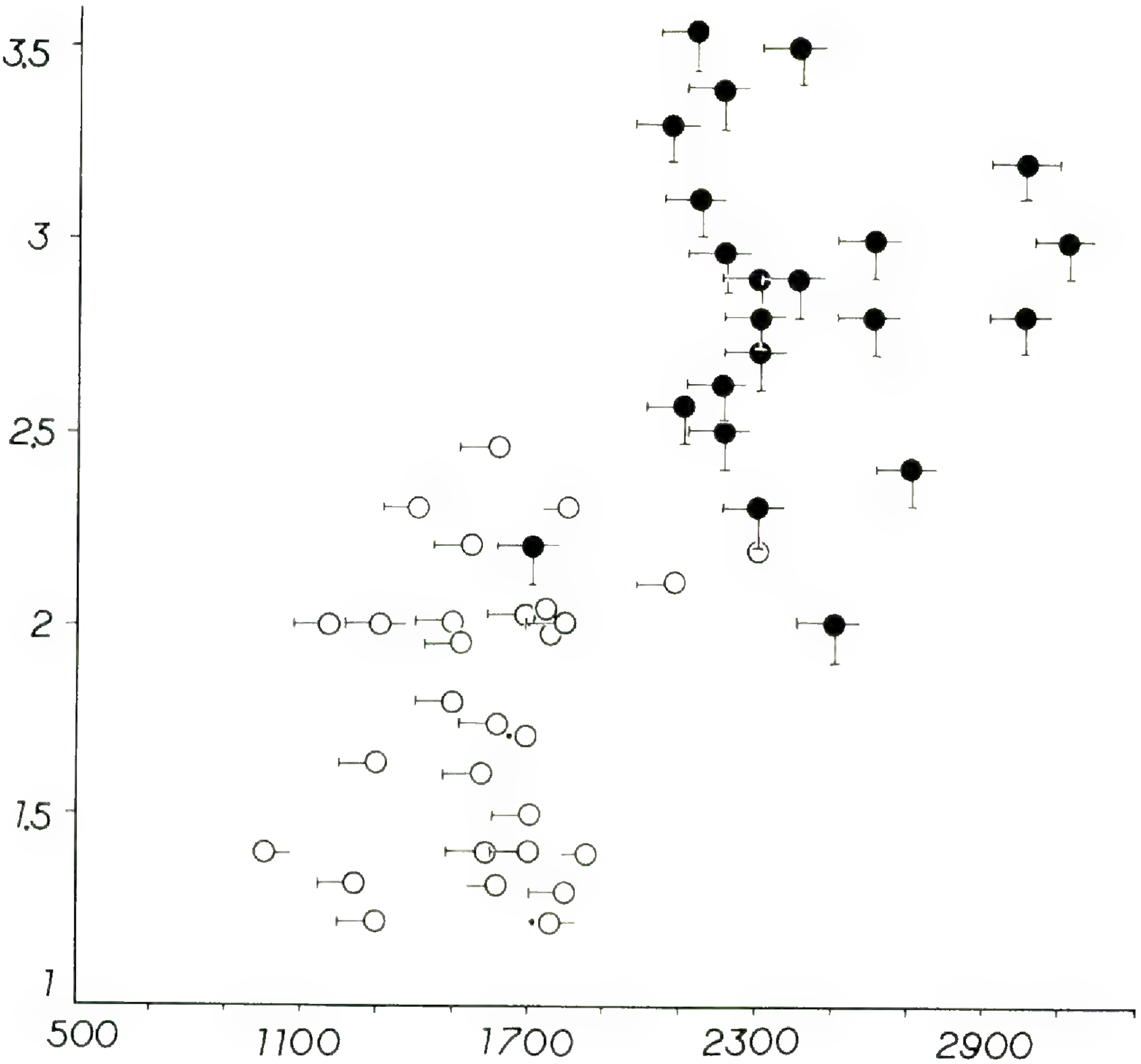


FIGURE 45. Scatter diagram showing variation between *Lyonia tuerckheimii* and *L. rubiginosa* var. *costata* in six characters. Vertical axis = twig thickness in mm. (measured near base of flowering or fruiting twigs); horizontal axis = elevation in meters; closed circle = twig ± densely pubescent, open circle = twig sparsely pubescent; full tail to left = capsules 5-merous, half tail to left = mixed 4- and 5-merous capsules, no tail to left = 4-merous capsules; full tail down = leaves very coriaceous, no tail down = leaves only slightly coriaceous, half tail down = intermediate; full tail to right = dense covering of unicellular hairs on midvein (abaxial leaf surface), half tail to right = sparse covering of unicellular hairs, no tail to right = unicellular hairs lacking on midvein. Small dots indicate character could not be scored.

Pinus occidentalis forests above approximately 2000 meters. Young plants often have quite slender twigs and small, narrowly acute leaves that are more strongly toothed than those of mature plants.

Rare hybrids between *Lyonia tuerckheimii* and *L. heptamera* or *L. urbaniana*, the other two species of *Lyonia* occurring in the high-elevation *Pinus occidentalis* forests of the Dominican Republic, have been collected in the Valle Nuevo area. They are probably to be found in less intensively collected areas, where these species occur together. These hybrids are discussed in

more detail under *L. heptamera* and *L. urbaniana;* their morphological characteristics are given in TABLE 10.

18. **Lyonia rubiginosa** (Pers.) G. Don, Gen. Hist. Dichl. Pl. **3:** 841. 1834.

Evergreen shrub to moderate-sized tree to 6(–10) meters tall, with brownish to gray, longitudinally furrowed bark. Twigs slightly to moderately angled, slender, sparsely to moderately lepidote, otherwise nearly glabrous to densely pubescent. Buds ovoid, 0.8–2.5 by 0.7–2 mm. Leaf blades elliptic to ovate, obovate, or nearly orbicular, 1.7–8(–9) by 0.7–4.2(–5.2) cm., ± flat to slightly acuminate, to acute, rounded, or truncate; base narrowly cuneate to rounded (rarely very slightly cordate); margin plane to slightly revolute, the distal portion strongly to obscurely and irregularly toothed, or entire, the proximal portion entire to irregularly and obscurely toothed; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely to densely pubescent on midvein, especially proximal portion, the 3° and higher order veins visible to obscure, the 2° veins prominent to obscure, sometimes depressed; abaxial surface moderately lepidote, otherwise glabrous to densely pubescent, the 3° and higher order veins obscure to very slightly raised, not forming dense, fine, raised network, the 2° veins obscure to slightly raised and visible; scales rust colored, persistent to deciduous, ca. 0.1–0.34 mm. in diameter, erose to entire; petiole 2–10 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, 4- to 16-flowered. Pedicels clearly articulated with calyx, slender, 4–11 mm. long, lepidote, otherwise glabrous to densely pubescent; bracteoles ± opposite, basal or nearly so, narrowly triangular, 0.7–2 mm. long; bracts to ca. 2 mm. long. Flowers 4- or 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 0.7–2 by 0.6–1.5 mm., the adaxial side glabrous or sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous to sparsely pubescent; corolla cylindrical, 4–8.5 by (2–)2.5–5 mm., white, occasionally pink tinged toward mouth, abaxially sparsely lepidote; filaments roughened, 3–5 mm. long, unappendaged or with very small spurs near anther-filament junction, anthers 0.7–1.8 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ellipsoid to ovoid, (3–)3.5–6.5 by 1.7–5 mm., slightly lepidote, otherwise sparsely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.4–3 mm. long.

DISTRIBUTION AND ECOLOGY. Hispaniola, Puerto Rico, and St. Thomas; open forests of *Pinus occidentalis* and thickets and cloud forests of various mountain ranges; ca. 250–2300 m. alt.

Key to the Varieties of *Lyonia rubiginosa*

1. Abaxial leaf surface often densely covered with unicellular hairs, or at least most plants with some leaves sparsely pubescent near margin or apex; capsules 3.5–5 mm. wide; [St. Thomas]. . . 18c. var. *rubiginosa.*

1. Abaxial leaf surface completely lacking unicellular hairs (but occasionally sparsely pubescent on midvein near petiole); capsules 1.7–3.5(–4) mm. wide.
   2. Leaves entire to obscurely (occasionally clearly) toothed, secondary veins obscure to slightly depressed; flowers mainly 5-merous, corolla 4–6 mm. long; [Puerto Rico] . . . . . 18b. var. *stahlii.*
   2. Leaves irregularly toothed or notched, secondary veins often depressed; flowers 5- and/or 4-merous, corolla (5.5–)6–8.5 mm. long; [Hispaniola] . . . . . 18a. var. *costata.*

18a. **Lyonia rubiginosa** (Pers.) G. Don var. **costata** (Urban) Judd, comb. et stat. nov.

Lyonia costata Urban, Symb. Antill. **7:** 316. 1912. *Xolisma costata* (Urban) Small, N. Am. Fl. **29**(1)**:** 71. 1914. TYPE: Dominican Republic, between Constanza and Valle Nuevo, 1700 m. alt., April 1910, *von Tuerckheim 3119* (holotype, B (destroyed); isotypes, F!, GH!, M!, MO!, NY!, L!, P!, S!, US (2 sheets)!).

Lyonia acutifolia Urban & Ekman in Urban, Ark. Bot. **20A:** 35. 1926. TYPE: Haiti, Massif de la Selle, Morne Tranchant, Pétionville, on the ridge toward Godet, ca. 1850 m. alt., 19 September 1924, *E. L. Ekman H1949* (holotype, S!; isotypes, GH!, IJ!, K!, NY!, S!, US (2 sheets)!).

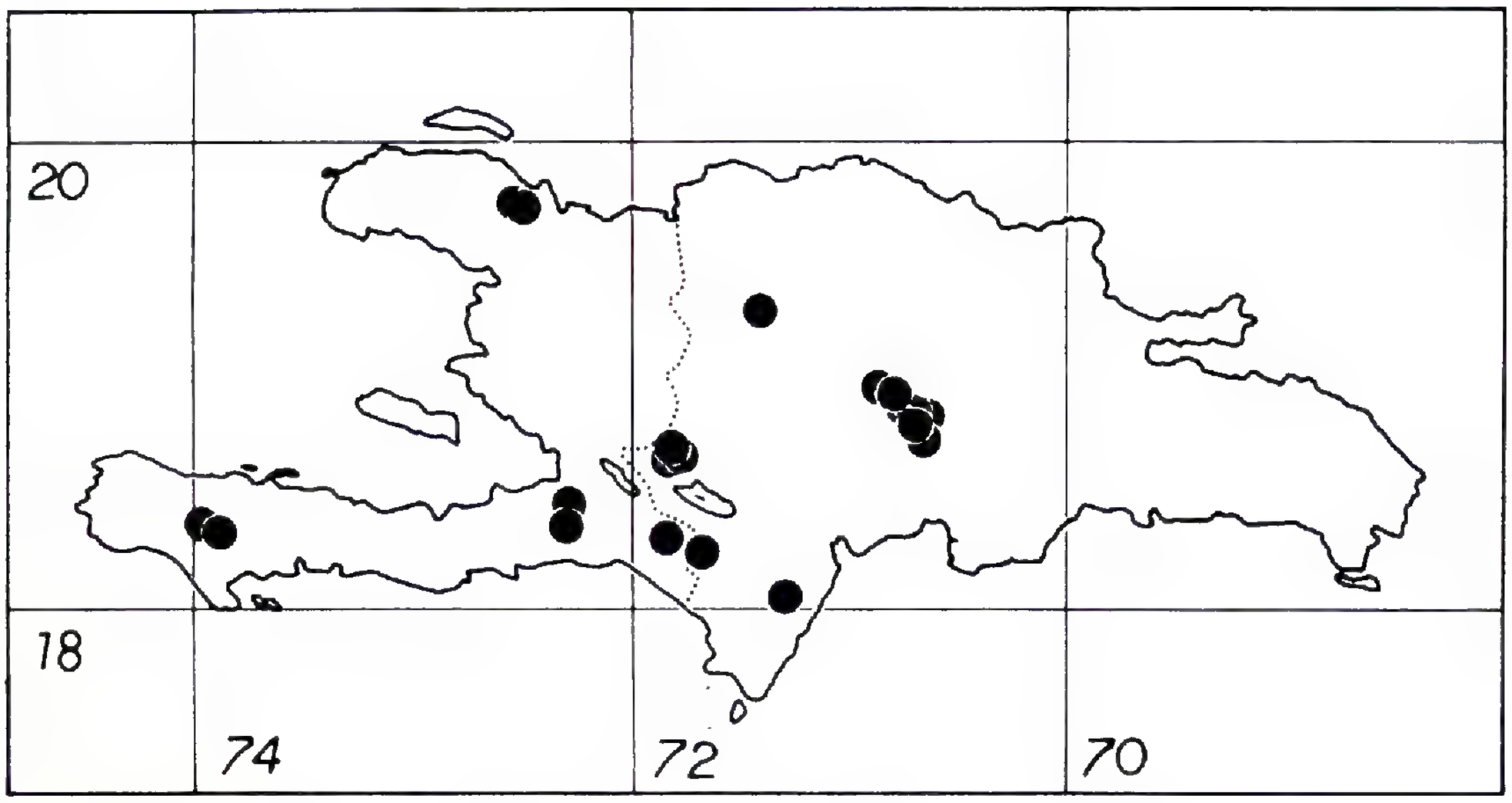
Lyonia angulata Urban & Ekman in Urban, Ark. Bot. **20A:** 35. 1926. TYPE: Haiti, Massif de la Selle, Morne Cabaio, Jardin Bois Pin, ca. 1900 m. alt., 25 August 1924, *E. L. Ekman H1632* (holotype, S!; isotypes, IJ!, S!, US!).

Lyonia darrasiana Urban & Ekman in Urban, Ark. Bot. **21A:** 52. 1927. TYPE: Haiti, Massif du Nord, near La Borgne, top of Morne Darras, ca. 1175 m. alt., 3 September 1925, *E. L. Ekman H4771* (holotype, S!; isotypes, IJ!, S!).

Xolisma longelaminata Sleumer, Repert. Sp. Nov. **36:** 271. 1934. *Lyonia longelaminata* (Sleumer) Jiménez, Rhodora **62:** 237. 1960. TYPE: Dominican Republic, Cordillera Central, prov. Santiago, Monción, Monte Gallo, ca. 1775 m. alt., 19 June 1929, *E. L. Ekman H12917* (holotype, S!; isotypes, A!, GH!, NY!).

Erect shrub to moderate-sized tree to 4(–10) meters tall. Twigs subglabrous to slightly pubescent. Leaf blades 2–6(–8.5) by 0.7–3(–5) cm.; margin distally strongly to obscurely and irregularly toothed, proximally entire to obscurely toothed; adaxial surface with 3° and higher order veins faintly visible to obscure, usually at least some 2° veins visible and slightly to moderately depressed; abaxial surface glabrous, occasionally sparsely pubescent on midvein (but not on lamina surface). Pedicels slender, 5–10 mm. long. Flowers 4- or 5-merous; calyx lobes 0.8–1.5(–2) by 0.8–1.3 mm.; corolla (5.5–)6–8.5 by (2–)2.5–4 mm. Capsule (3–)3.5–6 by 1.7–3.5(–4) mm. (FIGURES 43, 44.)

DISTRIBUTION AND ECOLOGY. Hispaniola, Cordillera Central, Massif du Nord, Sierra de Neiba, Massif de la Selle, and Sierra de Baoruco (including Monteada Nueva) (MAP 21). Low-elevation *Pinus occidentalis* forests, thickets, cloud



MAP 21. Distribution of *Lyonia rubiginosa* var. *costata*.

forests (of *Magnolia, Clusia, Cestrum, Miconia*); (900–)1100–2100(–2300) m. alt. Flowering probably late March through early May.

REPRESENTATIVE SPECIMENS. **Dominican Republic:** Cordillera Central, Constanza, top of Loma la Vieja, *Ekman H14043* (GH, S); La Matica, Constanza, *Ekman H13897* (A, F, S, US); Sierra de Neiba, between Hondo Valle and La Descubierta, Pyramid 200, *Jiménez et al. 5603* (HJ, NY, USD); Monteada Nueva, near Polo, *Judd & Liogier 1079* (A); between Constanza and Valle Nuevo, *Judd 1184–1192* (A); above La Nuez on rd. to Valle Nuevo, *Judd 1217* (A); La Rucilla, Manabao, Jarabacoa, *Liogier 12155* (JMB, NY); Cuatro Alas, NE. of La Culata, Constanza, *Liogier 13075* (GH, NY); Sierra de Neiba, La Doscientos, *Liogier 14615* (GH, IJ, JBM, NY, US); Las Aguas Blancas, Constanza, *Liogier & Liogier 21932* (JBM); above Los Arroyos, Pedernales, *Liogier & Liogier 23218* (JBM); El Convento, Constanza, *Marcano* [Herb. Jiménez No.] *5403* (HJ, NY, USD). **Haiti:** Massif du Nord, Bayaux, Morne Brigand, *Ekman H2967* (IJ, S); Massif de la Hotte, western group, Torbec, summit of ridge above La Mare-Proux, *Ekman H5324* (A, F, IJ, S, US); Massif de la Hotte, western group, Les Roseaux, Morne la Hotte, *Ekman H10659* (K, NY, S, US); Mornes des Commissaires, base of Guimbi Galata, *Holdridge 1773* (GH, MO, NY, US).

18b. **Lyonia rubiginosa** (Pers.) G. Don var. **stahlii** (Urban) Judd, comb. et stat. nov.

Lyonia stahlii Urban, Symb. Antill. **5:** 453. 1908. *Xolisma stahlii* (Urban) Small, N. Am. Fl. **29**(1): 71. 1914. TYPE: Puerto Rico, near Bayamón, in Monte Helechol, 500 m. alt., 1885, *A. Stahl 468* (holotype, B (destroyed); fragment of holotype, NY!).

Shrub to moderate-sized and often densely branched tree to 6(–10) meters tall. Twigs subglabrous to slightly (or rarely moderately) pubescent. Leaf

blades 1.7–6.5(–9) by 0.8–4(–5.2) cm.; margin distally obscurely and irregularly toothed to entire (less commonly strongly toothed), proximally entire to obscurely toothed; adaxial surface with the 3° and higher order veins faintly visible to obscure, the 2° veins obscure to visible, usually not depressed or only slightly so; abaxial surface glabrous, rarely sparsely pubescent on midvein near petiole (but not on lamina surface). Pedicels slender, 4–11 mm. long. Flowers (4- or) 5-merous; calyx lobes 0.7–1.5 by 0.6–1.2 mm.; corolla

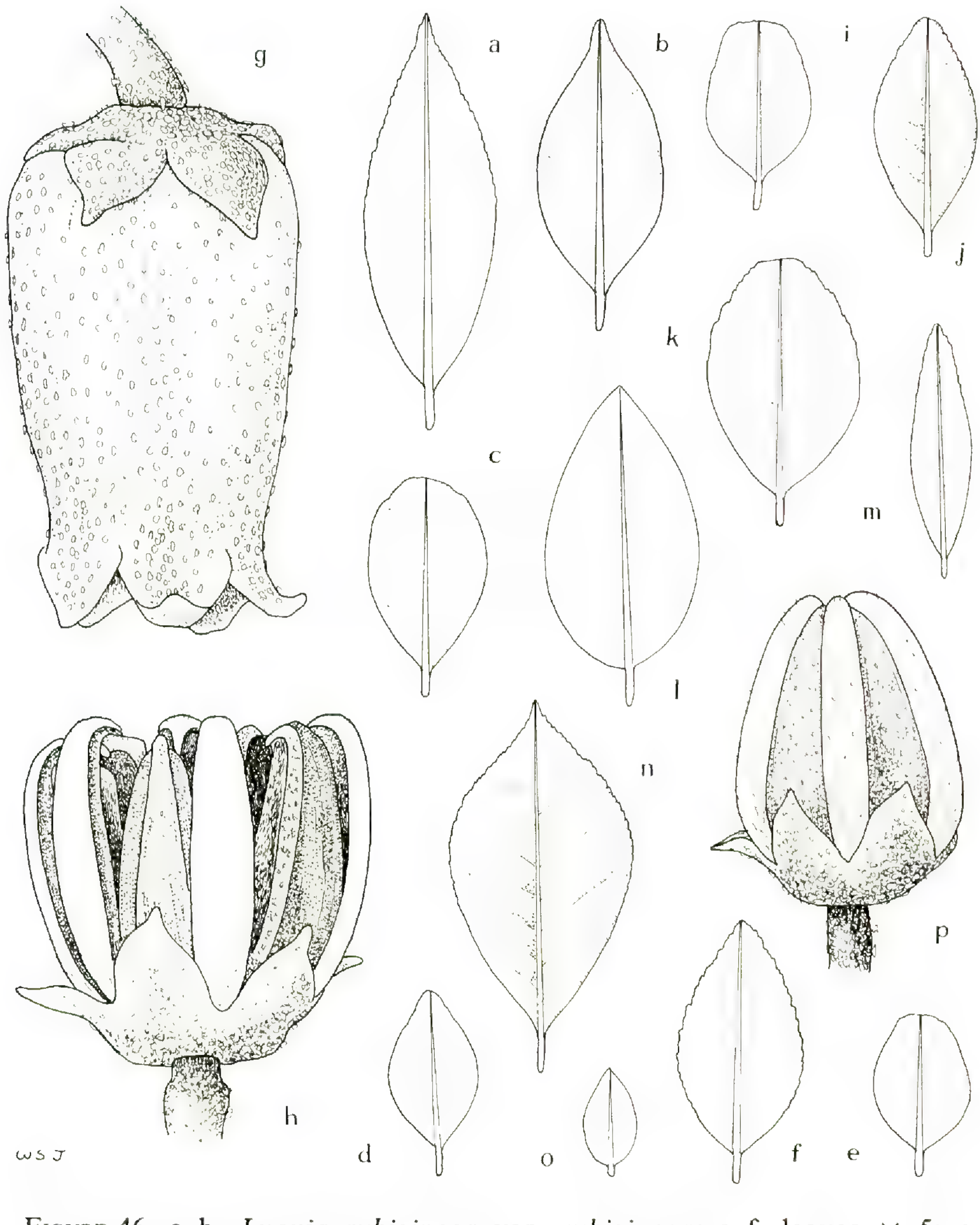


FIGURE 46. a–h, *Lyonia rubiginosa* var. *rubiginosa:* a–f, leaves, × .5; g, flower, × 6; h, capsule, × 6. i–p, *L. rubiginosa* var. *stahlii:* i–o, leaves, × .5; p, capsule, × 6.

4–6 by (2–)2.5–4 mm. Capsule 3.5–5.5 by 2–3.5(–4) mm. (FIGURE 46; see also Little *et al.* (1974).)

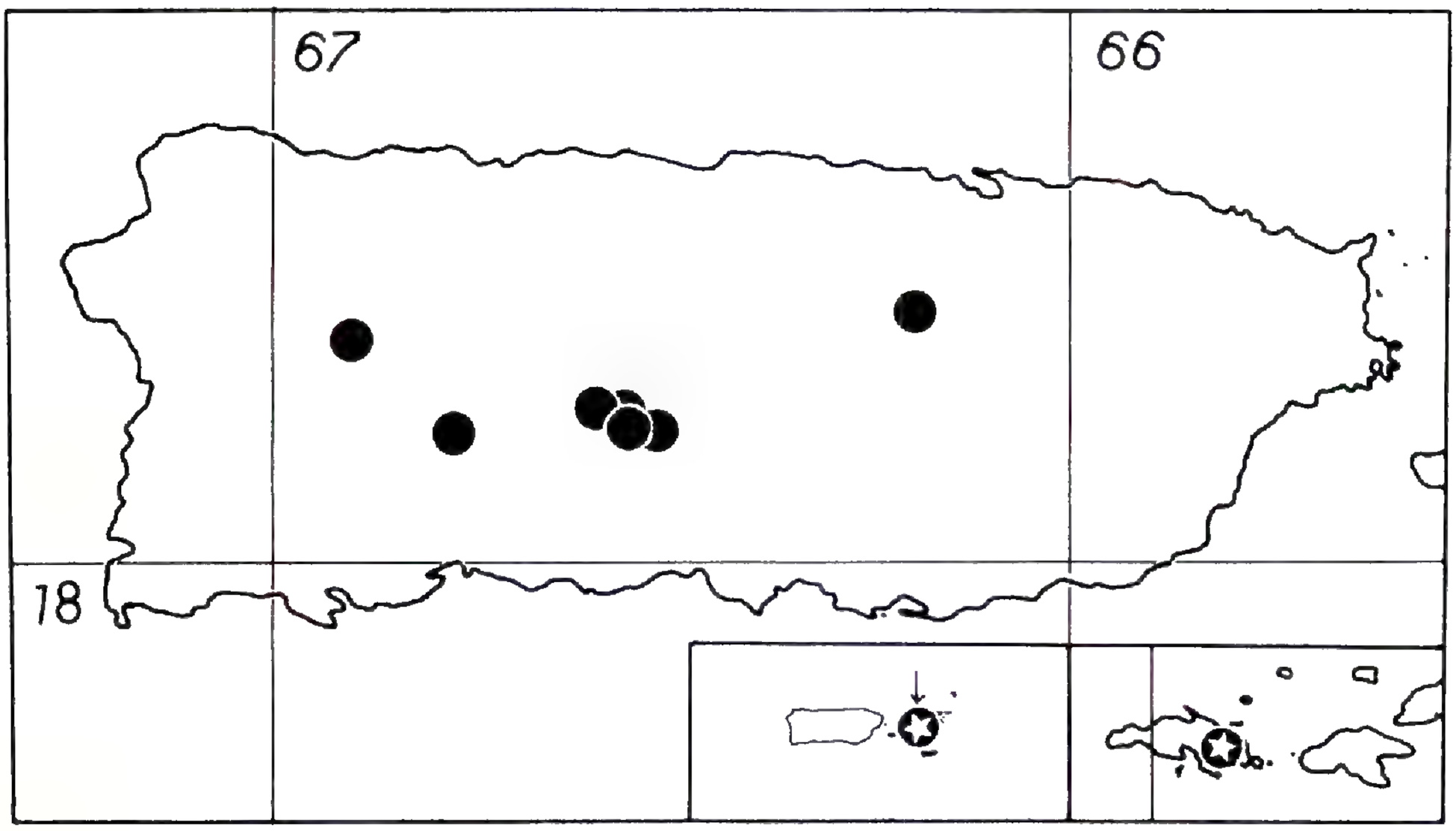
DISTRIBUTION AND ECOLOGY. Puerto Rico, Cordillera Central (MAP 22). Moist cloud forests, ca. (500–)1100–1338 m. alt. Locally common on highest peaks of range (Cerro de Punta, Monte Jayuya, Cerro Maravillas, Pico Guilarte) in dense thickets or forests of *Micropholis chrysophylloides, Clusia krugiana, C. gundlachii, Myrsine coriacea, Symplocos lanata, Calycogonium squamulosum, Ilex riedlaei, Miconia* spp. Also in ± disturbed roadside vegetation; seedlings common on road-cuts or landslides (if near seed-source). (See Gleason & Cook (1926) and Dansereau (1966) for more detailed discussion of vegetation of montane areas of Puerto Rico.) Flowering January through August.

REPRESENTATIVE SPECIMENS. **Puerto Rico:** Bosque Toro Negro, Cerro de Punta, *Howard & Nevling 15409* (A); Cerro de Punta, *Judd 512* (A); Monte Jayuya, near km. 17.7 on Rte. 143, *Judd 519* (A); Cerro Maravillas, near km. 21.3 on Rte. 143, *Judd 523* (A); Cerro de Punta, *Liogier 9546* (A, IJ, NY, US); summit of Pico Guilarte, Adjuntas, *Liogier 10022* (DUKE, GH, IJ, NY, US); 5 mi. SE. of Lares on Rte. 128, km. 48, *Little 21736* (GH, NY, US); headwaters of Inabon R., *Otero 761* (A, MO).

18c. **Lyonia rubiginosa** (Pers.) G. Don var. **rubiginosa**

Andromeda rubiginosa Pers. Syn. Pl. **1:** 481. 1805. *Xolisma rubiginosa* (Pers.) Small, N. Am. Fl. **29**(1): 68. 1914. TYPE: St. Thomas (lectotype (here designated), L!).

Andromeda pubescens Poiret in Lam. Encycl. Méth. Bot. Suppl. **1:** 355.



MAP 22. Distribution of *Lyonia rubiginosa* var. *stahlii* (dots) and *L. rubiginosa* var. *rubiginosa* (stars). Inset shows enlarged view of St. Thomas and adjacent islands.

1810. TYPE: St. Thomas, 1797, *Ledru 308* (holotype, P!; isotypes, P (3 sheets)!).

Shrub to small tree to ca. 4 meters tall. Twigs sparsely to densely pubescent. Leaf blades 2–8 by 0.9–4.2 cm.; margin distally obscurely and irregularly toothed to entire (less commonly clearly toothed), proximally entire to undulate; adaxial surface with the 3° and higher order veins usually visible, the 2° veins visible, usually not depressed; abaxial surface glabrous to densely pubescent. Pedicels slender, 4–8.5 mm. long. Flowers 5- (or 6-)merous; calyx lobes 1–2 by 0.7–1.5 mm.; corolla 5–8 by 3.5–5 mm. Capsule 4–6.5 by 3.5–5 mm. (FIGURE 46.)

DISTRIBUTION AND ECOLOGY. St. Thomas (MAP 22). Spiny thickets(?), ca. 250–300 m. Flowering December through March.

REPRESENTATIVE SPECIMENS. **St. Thomas:** near Bolongo, *Eggers s.n.*, Dec. 1886–Jan. 1887 (K, NY), *1482* (A, P); without definite locality, *Baudin s.n.*, 1797 (P), *Eggers 185* (NY, S), *Hornbeck s.n.* 1825–1844 (F), *Riedlé s.n.*, 1797 (P).

Lyonia rubiginosa is divided here into three geographically isolated varieties (MAPS 21 and 22). Variety *rubiginosa* is the most distinctive, being easily distinguished from vars. *stahlii* and *costata* by its leaves that are usually at least slightly pubescent on the abaxial surface, its often slightly larger flowers and/or fruits, and its frequently more pubescent twigs. Varieties *costata* and *stahlii* are obviously closely related and may be differentiated on characters such as degree of depression of secondary veins, prominence of marginal serrations, and corolla size (see key). The three taxa are recognized at the level of variety since they essentially differ only in a few characters of leaf morphology and in some slight size differences in the flowers and/or fruits—characters that are overall quite variable among the West Indian species. A few plants of var. *rubiginosa* completely lack unicellular hairs on the lower leaf surface; such plants are very similar to var. *stahlii*.

Lyonia rubiginosa is closely related to *Lyonia alainii*, *L. tuerckheimii*, and *L. truncata*. *Lyonia rubiginosa* vars. *costata* and *stahlii* differ from *L. alainii* in their ellipsoid to ovoid and more sparsely pubescent capsules, their cylindrical corollas, and their less coriaceous leaves. They are easily distinguished from *L. tuerckheimii* by their slender and usually only sparsely pubescent twigs, their different habit, their less robust capsules, and their thinner leaves with the secondary veins often depressed and with a lignified hypodermis only one cell thick (FIGURE 45). They differ from *L. truncata* in the lack of unicellular hairs on the abaxial leaf surfaces, and in the usually more prominent and depressed secondary veins of the leaves. *Lyonia rubiginosa* var. *costata* is altitudinally (and ecologically) isolated from *L. tuerckheimii*. It is found in low-elevation *Pinus occidentalis* forests, thickets, or moist cloud forests (FIGURES 5 and 45) up to ca. 2100 meters in the Cordillera Central and ca. 2000 meters in the Massif de la Selle, while *L. tuerckheimii* occurs at elevations above ca. 2000 meters in the ecologically quite different,

high-elevation *Pinus occidentalis* forests. (In the Massif de la Hotte, *L. rubiginosa* has been collected up to 2300 m. alt.; *L. tuerckheimii* is not known from that mountain range.) Variety *costata* is also altitudinally isolated from *L. truncata:* it occurs at elevations above approximately 1400 meters in the Cordillera Central and above approximately 1600 meters in the Massif de la Selle, while *L. truncata* has been collected up to 1200 meters in the Cordillera Central and to about 1600(–1700) meters in the Massif de la Selle (see FIGURES 5 and 6). *Lyonia rubiginosa* var. *costata* seems to be rare in the Sierra de Baoruco, where it has only been collected above Los Arroyos (in Lomas del Toro) near the Haitian border at an elevation of ca. 1800 meters, well above any known collection of *L. truncata* in this region. Variety *costata* is geographically isolated from *L. alainii* (MAPS 17 and 21), as var. *stahlii* is from all related taxa (MAP 22).

Lyonia rubiginosa var. *stahlii* is also similar to *L. jamaicensis,* a species endemic to Jamaica from which it can be distinguished by its usually sparsely pubescent twigs, its slightly smaller corollas, and its leaves that are usually about twice as long as wide, are sometimes more strongly toothed, and have secondary veins sometimes slightly depressed. In addition, these two taxa occur in quite different habitats. (It should be noted that a disjunct population in the mountains near Lares has more narrowly elliptic leaves than most specimens from the Cerro de Punta area and could easily be misidentified as *L. jamaicensis.*)

The geographically isolated *Lyonia rubiginosa* var. *rubiginosa* (see MAP 22) is usually easily distinguished from *L. alainii* and *L. tuerckheimii* since most plants have at least a few leaves that are pubescent abaxially. However, this variety can easily be confused with *L. truncata,* from which it differs in its often acuminate-tipped leaves that are more prominently reticulate-veined on the abaxial surface, and its slightly larger capsules.

Within *Lyonia rubiginosa* var. *costata* (and even within a single population—e.g., see *Judd 1184–1192*), there is great variation in leaf shape, size, apex, and secondary vein depression, as well as in prominence of the network of tertiary and higher order veins of the abaxial surface. This has led to the description of many species that clearly can no longer be maintained: as more collections have been made, populations have been studied in the field, and plants from diverse geographic areas and habitats have been compared, the total range and pattern of variability of the taxon has been revealed. It is interesting to note that flowers of populations of the Massif de la Hotte are characteristically four-merous, while those of the Massif de la Selle are usually mixed four- and five-merous on the same plants, and those of the Cordillera Central, Massif du Nord, Sierra de Neiba, and Monteada Nueva are chiefly five-merous. However, no other morphological characteristics studied are correlated with this variation.

Lyonia rubiginosa var. *stahlii* is also extremely variable in the size, shape (narrowly elliptic to nearly orbicular), apex type (acute to truncate), margin (entire to strongly toothed), and venation (obscure to visible and slightly depressed) of its leaves. This variation probably results from both genetic

and environmental effects. Plants in exposed, windswept conditions tend to have smaller, more entire-margined leaves, while shade leaves and leaves on rapidly growing sucker shoots are usually quite large; however, plants with very different leaf shapes can be found growing side by side under similar environmental conditions. In addition, the leaves increase in size (and often change shape) as the plant matures. Shading may also affect the luster and prominence of secondary veins and the angle at which the leaves are held in relation to the stem.

Lyonia rubiginosa var. *rubiginosa* was one of the earliest West Indian lyonias to be described, but this variety has not been collected since 1887. It has not been found again either in the hills above Bolongo or on the other slightly higher hills of St. Thomas, and it is possible that the variety is extinct. Although variation of this taxon is not well known, it seems to be especially great with respect to leaf size, marginal dentation, and pubescence.

Shrubs of *Lyonia rubiginosa* readily sucker from the base, especially after disturbance; the leaves of young shoots are often bright red due to the presence of anthocyanins, producing a strikingly beautiful contrast with the older, deep green leaves. Seedlings characteristically have very small, acute to acuminate, and more or less strongly toothed leaves.

19. **Lyonia jamaicensis** (Sw.) D. Don, Edinburgh New Philos. Jour. **17:** 159. 1834.

Andromeda jamaicensis Sw. Prodr. 73. 1788. *Cassandra jamaicensis* (Sw.) Niedz. Bot. Jahrb. **11:** 184. 1890. *Leucothoë jamaicensis* (Sw.) Ettingshausen, Blatt-Skel. Dikotyl. 93. *t. 38, figs. 2, 3.* 1861. TYPE: Jamaica, "alp.," *Swartz* (holotype, s!; isotypes, B-W (IDC 7440. 563: III. 5!), G-DC (IDC Herb. genevense 1373: I. 8!), L!, M!, S (3 sheets)!).

Andromeda fasciculata Sw. Prodr. **73:** 1788. *Lyonia fasciculata* (Sw.) G. Don, Gen. Hist. **3:** 831. 1834. *Xolisma fasciculata* (Sw.) Small, N. Am. Fl. **29**(1)**:** 69. 1914. TYPE: "in. mont.," *Swartz* (holotype, s!; isotypes, B-W (IDC 7440. 563: III. 4!), G-DC (IDC Herb. genevense 1373: II. 1!), M!, S (3 sheets)!).

Evergreen, erect shrub to moderate-sized tree to 7(–10) meters tall, with brownish to gray, longitudinally furrowed bark. Twigs moderately ridged, slender, sparsely lepidote, otherwise densely to sparsely pubescent. Buds ovoid, 0.6–2.5 by 0.5–1.5 mm. Leaf blades elliptic to slightly ovate or obovate, 2.5–8.5(–11) by 1–3(–5.5) cm., ± flat, coriaceous, ca. 0.27–0.34 mm. thick; apex acute to acuminate, rounded, or truncate, base narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to very obscurely toothed, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, densely pubescent on midvein, especially proximal portion, 3° and higher order veins faintly visible, 2° veins visible but usually not depressed; abaxial surface moderately lepidote, otherwise glabrous, the 3° and higher order veins ± flat or nearly so, often laxly reticulate, the 2° veins slightly

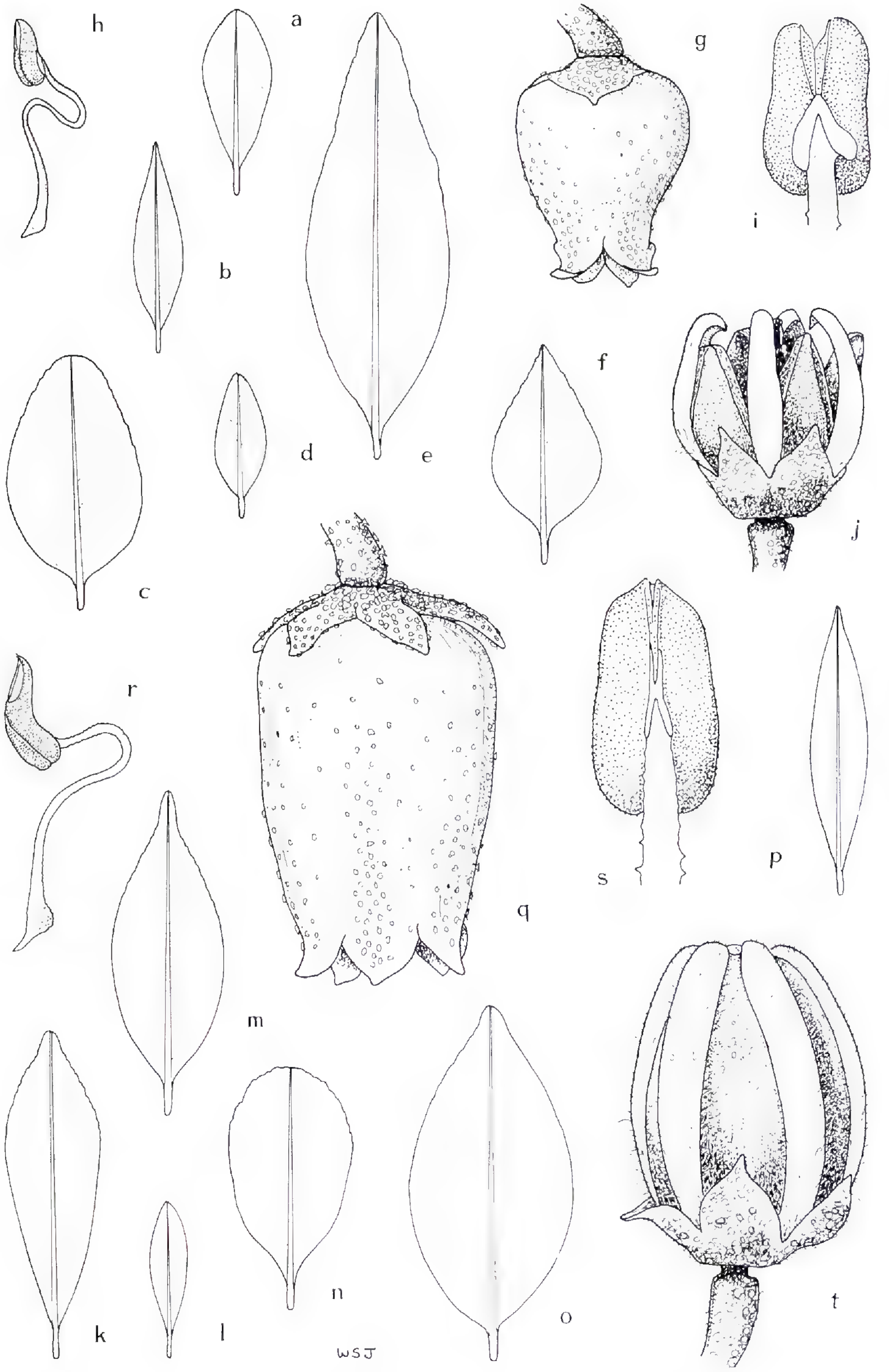
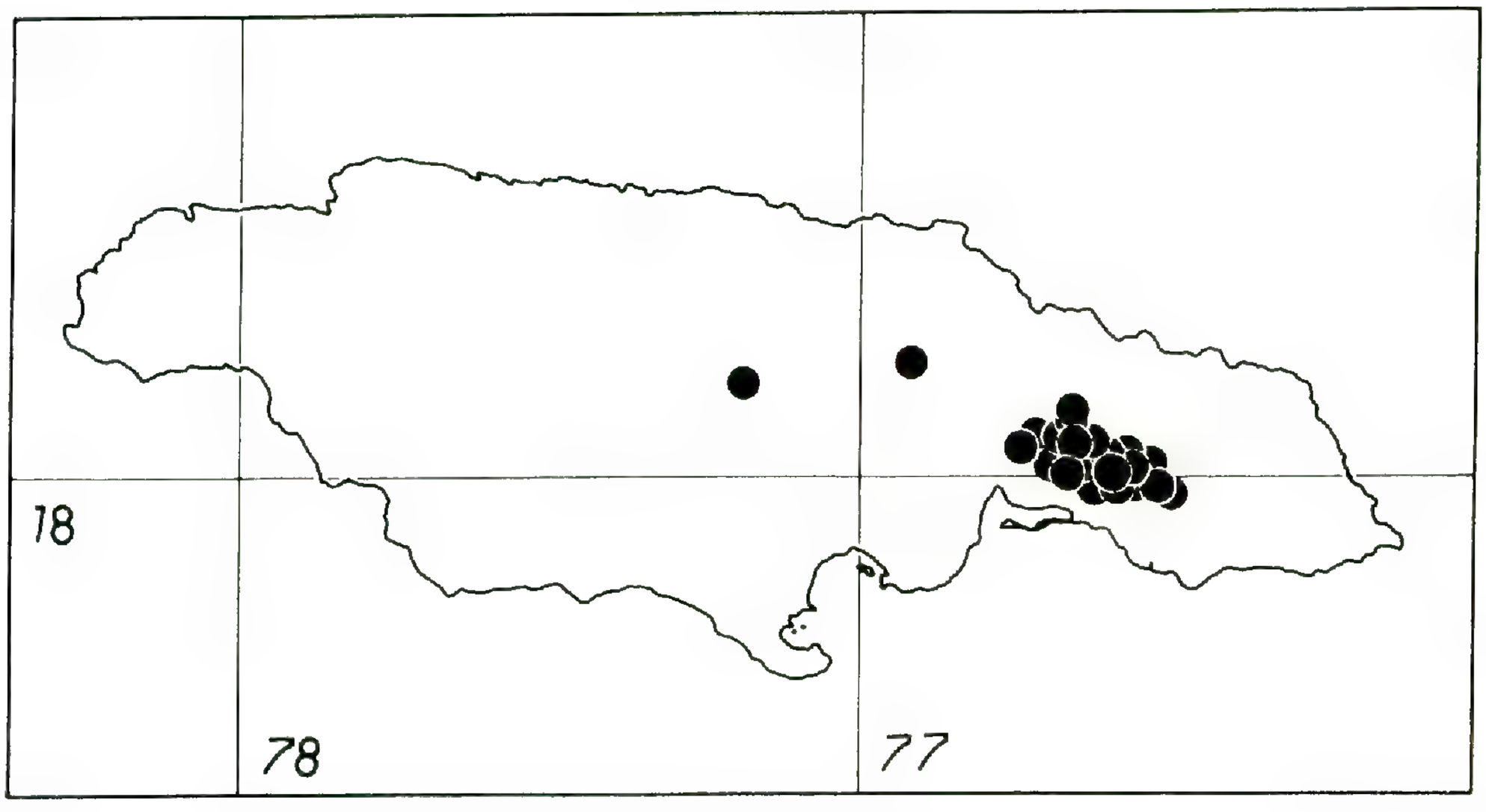


FIGURE 47. a–j, *Lyonia octandra:* a–f, leaves, × .5; g, flower, × 6; h, stamen, × 12.5; i, anther, × 25; j, capsule, × 6. k–t, *L. jamaicensis:* k–p, leaves, × .5; q, flower, × 6; r, stamen, × 12.5; s, anther, × 25; t, capsule, × 6.



MAP 23. Distribution of *Lyonia jamaicensis*.

raised to occasionally obscure; scales rust colored, becoming whitish with age, persistent, ca. 0.09–0.25 mm. in diameter, erose to nearly entire; petiole 3–14 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 5- to 15-flowered. Pedicels clearly articulated with calyx, slender, 4–11 mm. long, lepidote, otherwise glabrous to sparsely pubescent; bracteoles opposite to subopposite, basal or nearly so, narrowly triangular, 0.8–1.4 mm. long; bracts to ca. 2.5 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 1–2 by 0.6–1.3 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous or rarely sparsely pubescent near junction with pedicel; corolla cylindrical to less commonly long-urceolate, (4–)4.5–7 by (2–)2.5–4.5 mm., white, abaxially sparsely lepidote; filaments roughened, 3–4 mm. long, essentially unappendaged, anthers 0.8–1.1 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ellipsoid to ovoid, 4–6(–7) by 3–4 mm., slightly lepidote, otherwise sparsely to moderately pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–3 mm. long. (FIGURE 47; see also W. J. Hooker (1846).)

DISTRIBUTION AND ECOLOGY. Jamaica, chiefly southern slopes of Blue Mountains (MAP 23). Dry forests and thickets, (150–)300–1300 m. alt. Common in much-disturbed, open, shrubby communities of *Clusia, Lantana, Baccharis, Senecio, Ateramnus, Eugenia, Clethra, Rubus, Satureja* (ca. 500–1300 m.) ("dry slope forest" of Grubb and Tanner (1976); "montane sclerophyll" of Asprey & Robbins (1953)). Also occasionally in lower shale-hills vegetation; see Asprey and Robbins (1953). Locally common near 1200 m. alt. ("dry, evergreen thickets" of Asprey & Robbins (1953)), where vegetation lush

and species characteristic of "montane mist forest" at higher elevations mixed with those of dryer thickets below. (For extensive discussion of these vegetation types and lists of characteristic species, see Asprey & Robbins (1953) and Grubb & Tanner (1976).) Occasionally parasitized by *Dendropemon pauciflorus*. Flowering chiefly late May through early August.

REPRESENTATIVE SPECIMENS. **Jamaica.** CLARENDON PARISH: Bull Head, *Robbins 252* (UCWI). PORTLAND PARISH: trail NW. of Silver Hill Gap, *Hespenheide 785* (DUKE); near Green Hills, NW. of Hardwar Gap, *Judd 619* (A); between Section and Green Hill, *Judd 678* (A); between Green Hill and Wakefield, *Judd 679* (A). SAINT ANDREW PARISH: Greenwich Bridle Rd., *Adams 7491* (UCWI); below Irish Town, *Adams 8267* (DUKE, UCWI); Skyline Dr., Jacks Hill, *Adams 11757* (UCWI); Bellevue, *Asprey 1269* (UCWI); Gordon Town to Cinchona, Salt-Hill Pond, *Britton 25* (NY); Mavis Bank, *Harris 5856* (F, M, NY, UCWI); near Craigton, *Harris 8148* (M, UCWI); Liguanea Ridge, *Harris 12206* (F, GH, K, MO, NY, UCWI, US); Cinchona, *Hart 1280* (UCWI); ca. 2 mi. below Newcastle, *Hespenheide 1427* (DUKE, GH, MO, MSC, NY, UC, US); Irish Town, *Judd 596* (A); between Gordon Town and Guava Ridge, *Judd 625* (A); between Guava Ridge and Mavis Bank, *Judd 626* (A); Guava Ridge to Content Gap, *Judd 637* (A); St. Catherine Mt., *Papenfuss s.n.*, 27 June 1932 (UC); Clydesdale, trail to Cinchona, *Philipson 887* (MO); below Pine Grove, *Proctor 23674* (IJ, NY, US); Chestervale, *Proctor 23832* (IJ); banks of Yallahs R., *Purdie s.n.*, June 1843 (GH, K, P, S); Sky Ridge above Penfield, *Skelding 5458* (UCWI); St. Helen's Gap, *Tanner 440* (A); N. of Newcastle, *Webster 13692* (GH, IJ). ST. CATHERINE PARISH: Devil's Race Course, on Rte. B13 between Waterworks and Benbow, *Judd & Kress 639* (A); Devil's Race Course, *Proctor 7217* (GH). SAINT THOMAS PARISH: Arntully, *Adams 12241* (UCWI); near Sheldon, *Harris 5208b* (S, UCWI); ca. 1.5 mi. W. of Richmond Vale, *Judd 630* (A); Cedar Valley, *Judd 632* (A); Whitfield Hall to Portland Gap, *Judd 677* (A); near Farm Hill Gap, *Proctor 11413* (IJ).

Lyonia jamaicensis is closely related to *L. octandra*, from which it is fairly easily distinguished by its five-merous flowers with larger corollas, its longer capsules, its longer pedicels, its more densely pubescent twigs, and its less shredding bark. It may be confused with some forms of *L. rubiginosa* var. *stahlii*, from which it differs in the dense covering of unicellular hairs on its twigs, its leaves usually more than twice as long as wide and with less prominent secondary veins, and its slightly larger corollas. This species is altitudinally and ecologically isolated from *L. octandra*, occurring chiefly in the dry forest of the southern slopes of the Blue Mountains up to approximately 1300 meters, while *L. octandra* is found only at higher elevations (1450–2250 m.) in cloud forests or thickets.

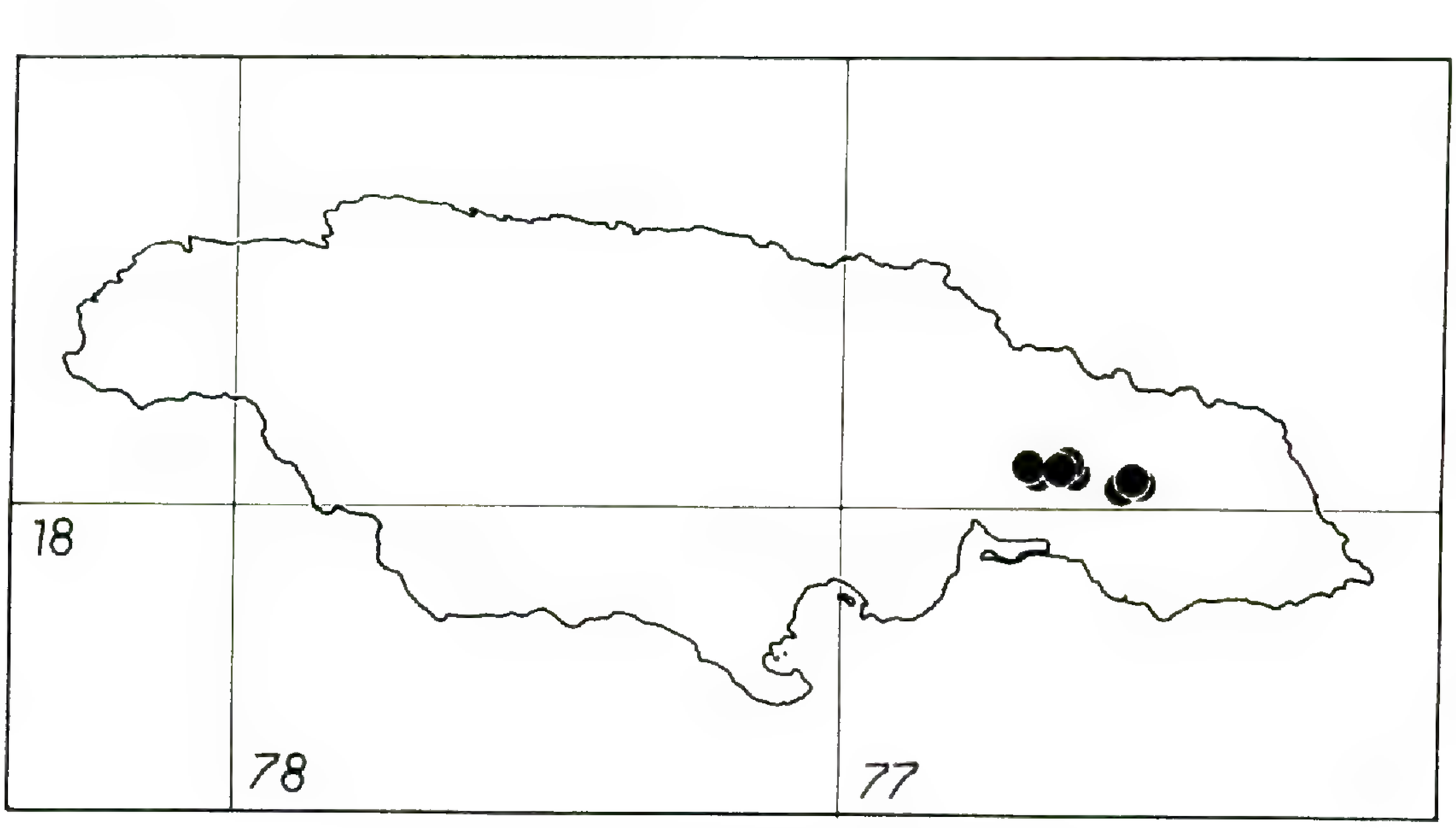
Seedlings tend to have smaller, narrower, and usually more acute or acuminate leaves than mature plants, and these leaves are borne on strongly ascending branches.

This taxon is correctly called *Lyonia jamaicensis*, the name selected by W. J. Hooker (1846) when he united *Andromeda jamaicensis* and *A. fasciculata*, both of which had been described by Swartz in his *Prodromus* (1788). As Hooker (1846, *t. 4273)* correctly noted, "the differences described in the two are no more than are evident in slight varieties of the same plant."

20. **Lyonia octandra** (Sw.) Griseb. Fl. Brit. W. Indian Is. 142. 1859.

Andromeda octandra Sw. Prodr. 73. 1788. *Xolisma octandra* (Sw.) Small, N. Am. Fl. **29**(1): 69. 1914. TYPE: Jamaica [probably collected in May, 1786, on trip to Blue Mountain Peak; see Stearn, 1980], *Swartz s.n.* (not seen).

Evergreen shrub to moderate-sized tree to ca. 11 meters tall, often densely branched, and with brownish or gray bark with long, sinuous, vertical furrows, often somewhat shredding. Twigs moderately ridged, slender, sparsely lepidote, otherwise glabrous or extremely sparsely pubescent. Buds ovoid, 0.6–2 by 0.5–1.3 mm. Leaf blades elliptic to ovate or slightly obovate, 2.5–6.5(–11) by 1–3.5(–4.5) cm., ± flat, coriaceous, ca. 0.23–0.31 mm. thick; apex acute to acuminate, rounded, or truncate; base narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to very obscurely toothed, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely to densely pubescent on proximal portion of midvein, with 3° and higher order veins obscure to visible, usually not depressed; abaxial surface sparsely to moderately lepidote, otherwise glabrous, the 3° and higher order veins ± flat, slightly and laxly reticulate to obscure, the 2° veins slightly raised to obscure; scales rust colored, becoming whitish with age, deciduous to persistent, ca. 0.17 mm. in diameter, entire to slightly irregular; petiole 2.5–7 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 3- to 10-flowered. Pedicels clearly articulated with calyx, slender, 1.5–4 mm. long, lepidote, otherwise usually sparsely pubescent; bracteoles ± opposite, basal, narrowly triangular, 0.7–1.4 mm. long; bracts to ca. 1.5 mm. long. Flowers 4-merous; calyx lobes triangular, with acuminate apices, 0.5–1.1 by 0.5–0.8 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial



MAP 24. Distribution of *Lyonia octandra*.

side lepidote, otherwise glabrous; corolla urceolate, 2.5–4 by 1.5–2.5 mm., white, abaxially sparsely lepidote; filaments roughened, 1–2.5 mm. long, unappendaged or with spurs to ca. 0.1 mm. long near anther-filament junction, anthers 0.4–0.9 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule short-ovoid, 2.5–4.3 by 2–3 mm., slightly lepidote, otherwise sparsely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.4–1.8 mm. long. (FIGURE 47.)

DISTRIBUTION AND ECOLOGY. Jamaica, Blue Mountains (MAP 24). Cloud forests, "montane mist forests," or thickets on high peaks; (1230–)1450–2250 m. alt. Shreve (1914), Grubb and Tanner (1976), and Tanner (1977) give detailed ecological studies of these forests. Coriaceous-leaved species of "mor ridge" forests, where *L. octandra* common, able to flourish due to ability to withstand low levels of nitrogen, phosphorus, and potassium found in highly acid soil (pH 2.5–3.5) of this forest type (Tanner, 1977). Frequently parasitized by *Dendropemon parvifolius* and *Dendrophthora opuntioides* (Grubb & Tanner, 1976). Seedlings found in undisturbed areas but more common on open, disturbed soil (e.g., banks along trail sides). Flowering mainly June to August.

REPRESENTATIVE SPECIMENS. **Jamaica.** PORTLAND PARISH: near Portland Gap, *Judd 648* (A). PORTLAND–SAINT ANDREW PARISH BORDER: Morce's Gap, *Purdie s.n.*, June 1843 (GOET, K, P); Mt. Horeb, *Weaver & Weaver 860* (DUKE, UCWI). SAINT ANDREW PARISH: New Haven Gap, *Johnson s.n.*, 29 June 1919 (F); John Crow Peak, *Tanner & Grubb 22* (A); 1/2 way between Morces Gap and John Crow Peak, *Tanner 502* (A); John Crow ridge, *Tanner & Grubb 62* (A); near Hardwar Gap, *Judd 605* (A). ST. THOMAS PARISH: between Blue Mt. Peak and Portland Gap, *Crosby et al. 893* (DUKE, GH, UC, UCWI); trail from Portland Gap to Blue Mt. Peak, *Judd 652* (A); along trail from Whitfield Hall to Portland Gap, *Judd 653* (A); near Blue Mt. Peak, *Judd 658* (A).

Lyonia octandra is closely related to *L. jamaicensis*, from which it can be easily distinguished by its four-merous flowers with smaller corollas, its smaller capsules, its shorter pedicels, its often shredding bark, and its more or less glabrous twigs. In addition, leaves of flowering or fruiting shoots are often smaller than those of *L. jamaicensis*. *Lyonia octandra* is altitudinally and ecologically isolated from *L. jamaicensis* (FIGURE 4). There is a gap of ca. 300 meters between the highest-elevation populations of *L. jamaicensis* and the lowest of *L. octandra* in the region around Blue Mountain Peak, but in the Mt. Horeb–Hardwar Gap area this separation is narrowed to about 50 meters, with *L. octandra* in moist montane forests and *L. jamaicensis* in the slightly drier evergreen thickets. *Lyonia octandra* is also similar to the Cuban species *L. trinidadensis*, from which it differs in its short-ovoid capsules, its nearly glabrous twigs, and its slightly smaller corollas.

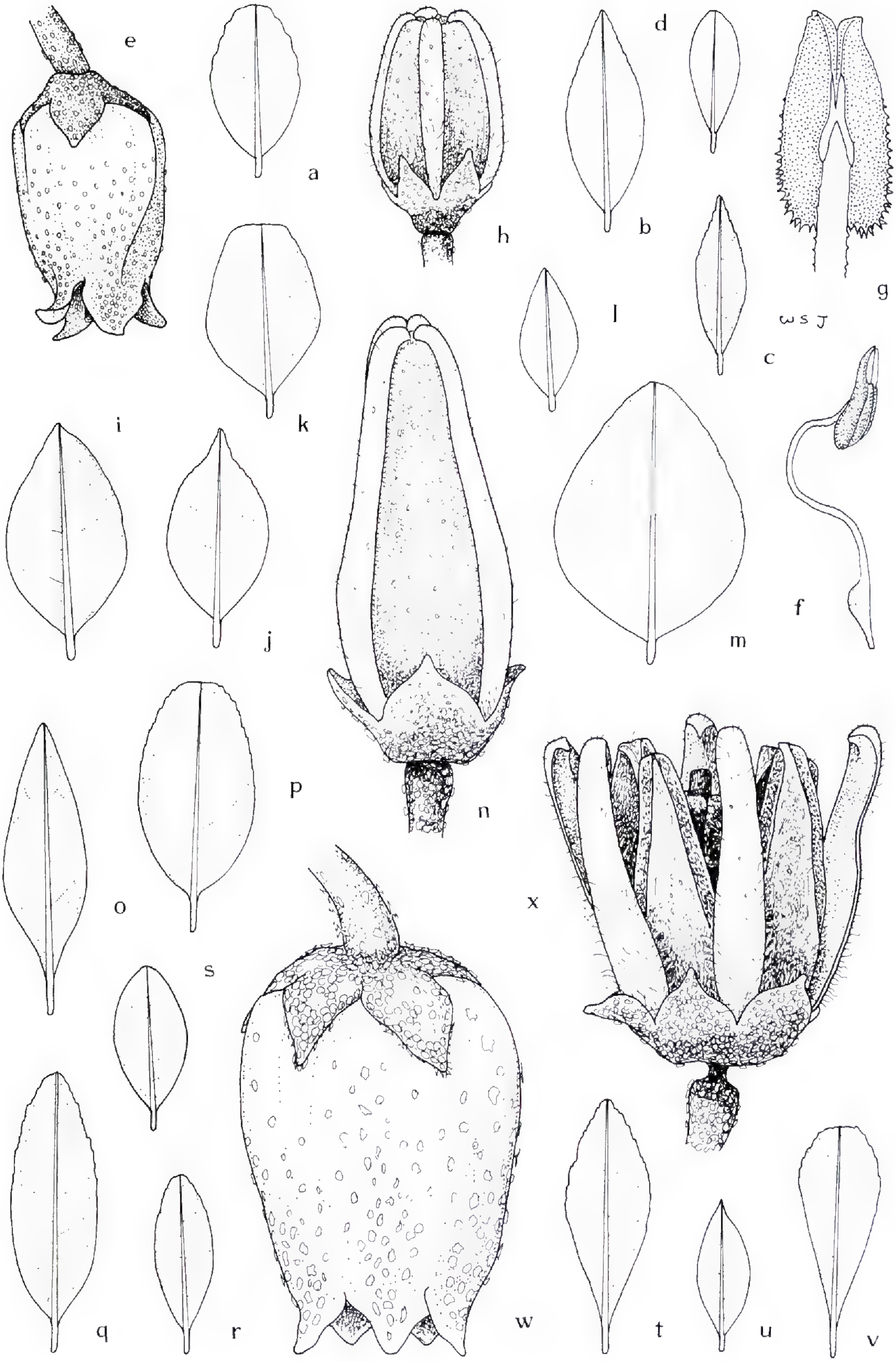
21. **Lyonia trinidadensis** Judd, sp. nov.

Frutices sempervirentes ad 2–3 m. alti; ramuli hornotini moderate angulati, graciles, lepidoti, pilis unicellularibus sparsim vel dense vestiti. Folia elliptica,

ovata vel obovata, 2–6 cm. longa, 0.9–2.5(–3) cm. lata, coriacea; ad apicem acuta vel fere acuta, acuminata, rotundata, vel truncata; ad basin anguste cuneata, late cuneata vel rotundata; margo planiuscula vel leviter revoluta, in parte distali integra, undulata, vel subdentata, in parte proximali integra; nervus primarius prominens; nervi secundarii obscuri vel leviter manifesti; pagina abaxialis lepidota non pilifera; petioli 2.5–5 mm. longi. Inflorescentiae fasciculatae, cum ca. 3 ad 15 floribus. Pedicelli graciles cum calyce articulatis, 2.5–4.5 mm. longi. Flos plerumque 4-merus. Calyx lobis 0.8–1.2 mm. longis, 0.5–0.8 mm. latis. Corolla urceolata vel plus minusve cylindracea, 3–4.5 mm. longa, 1.5–3 mm. lata, alba, sparsim lepidota in pagina abaxiali. Filamenta 2–2.5 mm. longa, haud calcarata vel cum calcaribus duobus minutis prope apicem; antherae ca. 0.9 mm. longae. Capsula anguste ovoidea, 3.5–5 mm. longa, 1.7–3 mm. lata, pilis unicellularibus sparsim vel moderate vestita.

Evergreen shrub to 2 or 3(?) meters tall, with gray, longitudinally furrowed bark. Twigs moderately ridged, slender, moderately lepidote, otherwise sparsely to densely pubescent. Buds ovoid, 0.6–1.5 by 0.6–1.2 mm. Leaf blades elliptic to ovate or obovate, 2–6 by 0.9–2.5(–3) cm., ± flat, coriaceous, ca. 0.25–0.33 mm. thick; apex acute, acuminate to rounded or truncate; base narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to obscurely and irregularly toothed, proximal portion entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely to densely pubescent on midvein, especially proximal portion, the 3° and higher order veins faintly visible to obscure, the 2° veins obscure to slightly visible, not depressed; abaxial surface moderately lepidote, otherwise glabrous, occasionally very sparsely pubescent on extreme proximal portion of midvein (but not on lamina surface), the 3° and higher order veins ± flat, slightly and laxly reticulate to obscure, the 2° veins obscure to slightly visible; scales ± rust colored, becoming whitish with age, deciduous to persistent, ca. 0.09–0.27 mm. in diameter, entire to slightly erose; petiole 2.5–5 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, 3- to 15-flowered. Pedicels clearly articulated with calyx, slender, 2.5–4.5 mm. long, lepidote, otherwise glabrous to sparsely pubescent; bracteoles ± opposite, basal, narrowly triangular, 0.6–1.2 mm. long; bracts to ca. 1.5 mm. long. Flowers 4- (or 5-)merous; calyx lobes triangular, with acuminate apices, 0.8–1.2 by 0.5–0.8 mm., the adaxial side glabrous or sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous to very sparsely pubescent near base; corolla urceolate to cylindrical, 3–4.5 by 1.5–3 mm., white, abaxially sparsely lepidote; filaments roughened, 2–2.5 mm. long, unappendaged or with minute spurs near anther-

FIGURE 48. a–h, *Lyonia trinidadensis:* a–d, leaves, × .5; e, flower, × 6; f, stamen, × 12.5; g, anther, × 25; h, capsule, × 6. i–n, *L. elliptica:* i–m, leaves, × .5; n, capsule, × 6. o–x, *L. affinis:* o–v, leaves, × .5; w, flower, × 6; x, capsule, × 6.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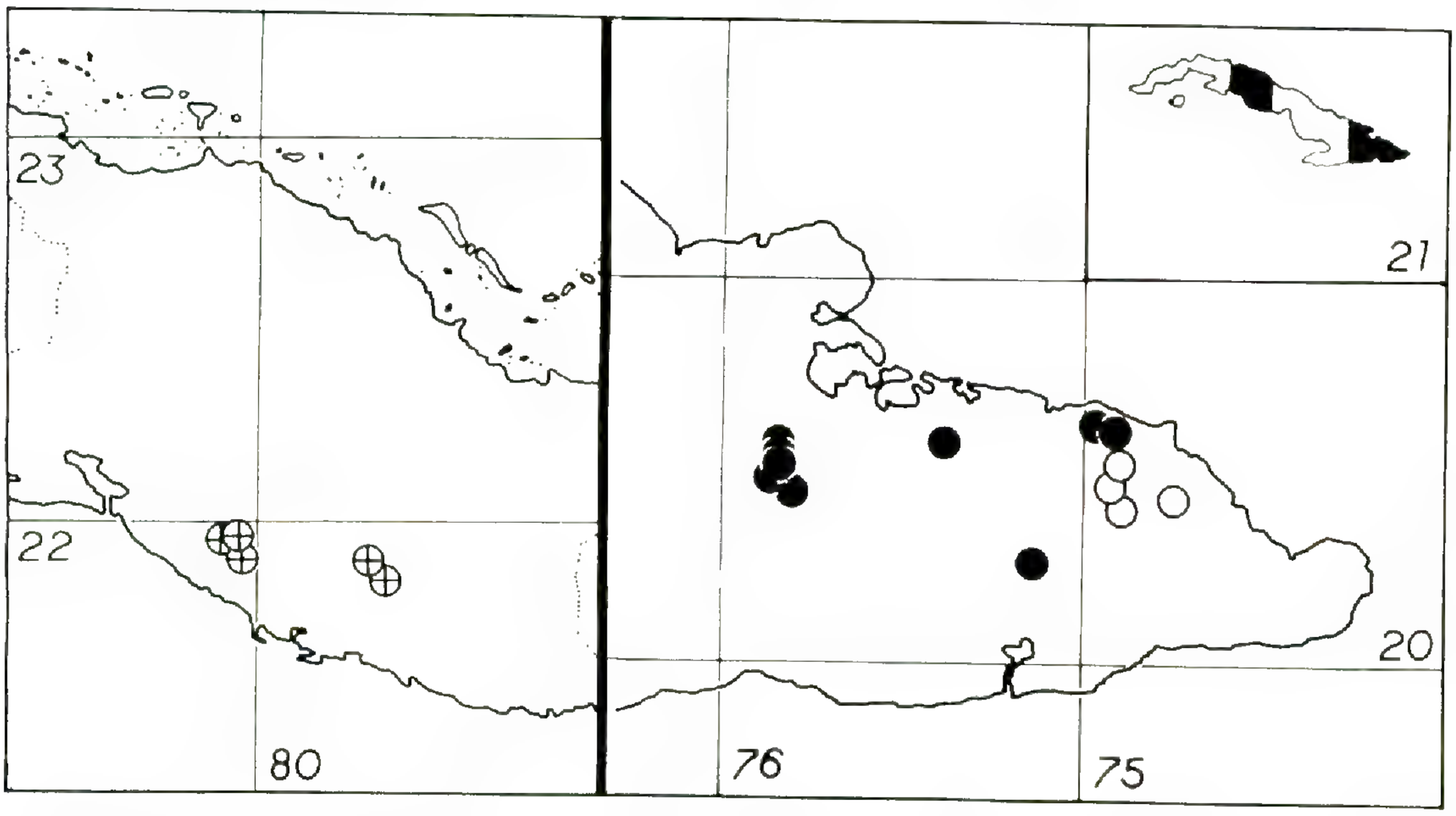


MAP 25. Distribution of *Lyonia trinidadensis* (circles with cross), *L. nipensis* var. *nipensis* (dots), and *L. nipensis* var. *depressinerva* (circles).

filament junction, anthers ca. 0.9 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule long-ovoid, 3.5–5 by 1.7–3 mm., slightly lepidote, otherwise sparsely to moderately pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds ca. 2 mm. long. (FIGURE 48.)

TYPE: Cuba, prov. Las Villas, savanna near Buenos Aires, 820 m., Trinidad Mts., July 1929, *Bro. León, Jack, & Rome 13964* (holotype, NY!; isotype, GH!).

DISTRIBUTION AND ECOLOGY. Cuba, Las Villas Prov., Sierra de Trinidad (incl. Sierra de San Juan) and Sierra de Sancti Spiritus (MAP 25). Cloud forests and savannas, ca. 700–1070 m. alt. Flowering July and August.

REPRESENTATIVE SPECIMENS. **Cuba.** LAS VILLAS PROV.: Trinidad Mts., El Porvenir to Aguacate, *Britton 5340* (NY); Trinidad Hills, Buenos Aires, *Jack 7874* (A, S, US); Banao Mts. [= Sierra de Sancti Spiritus], Loma de los Helechales, *Bros. León & Clemente 5388* (NY); Banao Mts., La Gloria Hill, *Bro. León & Roig 8008* (GH, NY); Trinidad Mts., Buenos Aires, vicinity of Sopapo, *Smith et al. 3351a* (GH).

Lyonia trinidadensis is similar to *L. octandra* but differs in its long-ovoid capsules, its more densely pubescent twigs, and its slightly larger corollas. Some plants also superficially resemble *L. jamaicensis*. It does not seem to be especially close to any of the other Cuban species, although some forms of *L. affinis*, *L. elliptica*, or *L. myrtilloides* are perhaps most similar.

Specimens of this species from the Sierra de Trinidad have usually been identified as *Lyonia elliptica*, but the type of this name (*C. Wright 2197*,

in part, collected in Oriente) is clearly a different species. They differ from this specimen in having leaves often smaller, with various differences in anatomy (see TABLE 8) and venation, and lacking unicellular hairs on the abaxial surface; much smaller capsules; and often more densely pubescent twigs. Small's (1914) concept of *L. elliptica* was very broad; it included all of *L. trinidadensis,* part of *L. affinis,* and what is here considered to be *L. elliptica* (i.e., *Wright 2197,* in part; a very rare and poorly known taxon). Since the morphological differences separating *L. elliptica* sensu stricto from the populations of the Trinidad Mountains are of a magnitude comparable to those separating many Cuban species, it is clear that they should be considered to represent separate species. Thus, the Sierra de Trinidad plants are left without a name. Because this taxon is the only species of *Lyonia* in the Sierra de Trinidad of Las Villas province, I am naming it *Lyonia trinidadensis.*

22. **Lyonia affinis** (A. Rich.) Urban, Repert. Sp. Nov. **22:** 44. 1925.

Leucothoë affinis A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11:** 74. 1850 [1851]. *Xolisma affinis* (A. Rich.) Small, N. Am. Fl. **29**(1): 69. 1914. TYPE: Cuba [prov. Oriente], Sierra Maestra, Pinal, Santiago de Cuba, 650 hexap. alt., April 1844, *J. Linden 1694* (holotype, P?; isotypes, F (fragment of isotype at P)!, GH!, K!, L (fragment of isotype at P)!, NY (2 sheets)!, NY (fragment of isotype at K)!, P!, W!).

Leucothoë myrsinifolia A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11:** 1850 [1851]. *Lyonia jamaicensis* (Sw.) D. Don var. *myrsinifolia* (A. Rich.) Griseb. Catal. Pl. Cubens. 50. 1866. *Andromeda jamaicensis* Sw. var. *myrsinifolia* (A. Rich.) Gómez de la Maza, Anal. Hist. Nat. Madrid **19:** 250. 1890. *Xolisma myrsinifolia* (A. Rich.) Small, N. Am. Fl. **29**(1): 68. 1914. *Lyonia myrsinifolia* (A. Rich.) Urban, Repert. Sp. Nov. **22:** 45. 1925. TYPE: Cuba, [prov. Oriente], Cerro de Cobre, Santiago de Cuba, July 1844, *J. Linden 2056* (holotype, P!; fragment of holotype, F!; isotype, P!; fragment of isotype, L).

Xolisma brittonii Small, N. Am. Fl. **29**(1): 71. 1914. *Lyonia brittonii* (Small) Urban, Repert. Sp. Nov. **22:** 41. 1925. TYPE: Cuba, prov. Oriente, vicinity of El Cuero, 400 m. alt., 18–19 March 1912, *Britton & Cowell 12773* (holotype, NY!; isotypes, F!, GH!, HAC?, NY (2 sheets)!, US!).

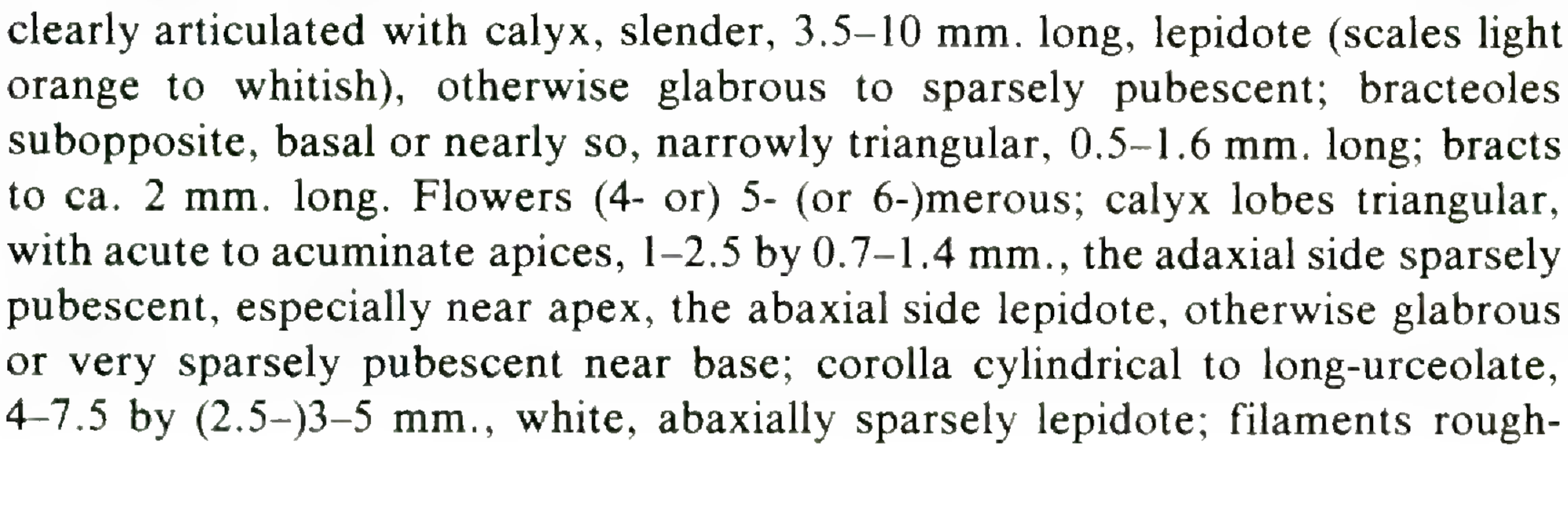
Lyonia acutata Urban, Repert. Sp. Nov. **22:** 44. 1925. TYPE: Cuba, [prov. Oriente], Sierra Maestra, Pinal, Santiago de Cuba, 650 hexap. alt., April 1844, *J. Linden 1694,* in part (holotype, B (destroyed)).

Lyonia papayoensis Urban, Repert. Sp. Nov. **22:** 44. 1925. TYPE: Cuba, prov. Oriente, in Sierra Maestra, Pinar de Papayo, ca. 700 m. alt., 22 June 1918, *E. L. Ekman 9250* (holotype, s!; fragment of holotype, NY!).

Lyonia bayamoensis Urban, Repert. Sp. Nov. **22:** 43. 1925. TYPE: Cuba, prov. Oriente, near Bayamo in Pinar de Corojo, ca. 400 m. alt., 22 March 1915, *E. L. Ekman 5060* (holotype, s!; isotypes, NY!, s!).

Evergreen shrub to ca. 3 meters tall, with gray, longitudinally furrowed bark(?). Twigs moderately angled, slender, moderately lepidote, otherwise glabrous to densely pubescent. Buds ovoid, 1–2 by 0.8–1.2 mm. Leaf blades

elliptic to ovate or obovate, 2.5–7 by 0.9–3.5(–4.5) cm., ± flat, coriaceous, ca. 0.3–0.4 mm. thick; apex acute to rounded, truncate, or very slightly acuminate; base attenuate, narrowly to broadly cuneate or occasionally rounded; margin plane to slightly revolute, distal portion entire to clearly and irregularly toothed, proximal portion entire to undulate; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely to moderately pubescent on midvein, especially proximal portion, the 3° and higher order veins visible to obscure, the 2° veins usually visible, more prominent than 3° veins, often clearly connected in series of arches, rarely obscure, not depressed; abaxial surface moderately lepidote, otherwise densely to moderately pubescent (occasionally sparsely pubescent near margin or apex of blade), the 3° and higher order veins ± flat or nearly so, slightly and laxly reticulate to obscure, the 2° veins usually visible and connected together in series of arches or occasionally obscure; scales rust colored, becoming whitish with age, deciduous to persistent, ca. 0.08–0.27 mm. in diameter, erose to entire; petiole 3–10 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 3- to 12-flowered. Pedicels clearly articulated with calyx, slender, 3.5–10 mm. long, lepidote (scales light orange to whitish), otherwise glabrous to sparsely pubescent; bracteoles subopposite, basal or nearly so, narrowly triangular, 0.5–1.6 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acute to acuminate apices, 1–2.5 by 0.7–1.4 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous or very sparsely pubescent near base; corolla cylindrical to long-urceolate, 4–7.5 by (2.5–)3–5 mm., white, abaxially sparsely lepidote; filaments rough-



MAP 26. Distribution of *Lyonia affinis* (circles), *L. elliptica* (diamonds), and *L. macrophylla* (dots).

ened, 3–5.5 mm. long, unappendaged or with minute spurs near anther-filament junction, anthers 0.7–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to ellipsoid, 3.5–7.5 by 3–4.5 mm., sparsely lepidote, otherwise sparsely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–4 mm. long. (FIGURE 48.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra Maestra (MAP 26). Pinelands (*Pinus maestrensis*) and thickets, ca. 400–700(?) m. alt. Flowering January, March, April, July, and October.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: S. slopes of Pico Turquino, Sierra Maestra, *Acuña 14509* (US); vic. of El Cuero, *Britton & Cowell 12764* (F, GH, MO, NY, S, US); El Cobre, near mine, *Ekman 7894* (NY, S); steep hillsides, Cobre, *C. Wright 1635,* in part (GH, GOET, K, MO, NY, P).

Lyonia affinis is probably closely related to the poorly known *L. elliptica,* from which it differs in its five-merous flowers with larger corollas and its wider capsules. Some plants are also quite similar to *L. macrophylla,* from which they can easily be distinguished by the unicellular hairs on the abaxial leaf surface, the more cylindrical corollas, and the often narrower, more acute, shorter-petioled leaves. *Lyonia affinis* is geographically isolated from the above taxa since neither occurs in the Sierra Maestra. Because *L. affinis* is a morphologically generalized species, it is quite similar to several taxa of other West Indian Islands. It could easily be confused with *L. rubiginosa* var. *rubiginosa* or with *L. truncata,* except that the leaves of the two species differ in anatomy (TABLE 8) and venation pattern, as well as slightly in shape. *Lyonia jamaicensis* also could easily be confused but for its lack of unicellular hairs on the abaxial leaf surface.

Lyonia affinis is extremely variable in leaf shape (elliptic to obovate), size, apex type (rounded to acute), margin (entire to strongly toothed), and pubescence (very sparsely to densely covered with unicellular hairs abaxially), but all intermediates exist, and the variation follows no geographic or ecological pattern. These differences have led to the description of several taxa that are essentially only extremes within the total range of variation and that are here reduced to synonymy. For example, the types of *L. brittonii* and *L. papayoensis* are only forms with clearly toothed leaves, and the type of *L. myrsinifolia* is a plant with small leaves that are usually acute at the apex.

I have chosen the name *Lyonia affinis* over *L. myrsinifolia,* which was also described as new by A. Richard in the same publication (Sagra, 1850) because the name *L. myrsinifolia* has usually been used to refer to a very different and only distantly related taxon of the Sierra de Nipe, here called *L. glandulosa* var. *glandulosa.* To take up the name *L. myrsinifolia* for this taxon of the Sierra Maestra would lead to confusion for those using the earlier literature.

The name *Lyonia acutata* Urban is based on a specimen of *Linden 1694,*

as is the earlier name *Leucothoë affinis* A. Rich. Urban (1925) evidently thought that Richard's collection was a mixture of two species, since he listed the differences between his new species and *Lyonia affinis*. These differences (e.g., leaf shape and sepal length and width) are very slight and are well within the observed variation of this species.

23. **Lyonia elliptica** (C. Wright ex Small) Alain, Rev. Soc. Cuba Bot. **13:** 61. 1956.

Xolisma elliptica C. Wright ex Small, N. Am. Fl. **29**(1): 68. 1914. TYPE: Cuba, [prov. Oriente], Monte Verde, in dense woods, 18 July [probably 1860 or 1861], *C. Wright 2197*, in part (holotype, NY!; isotypes, GOET!, GH!, L (fragment from P)!, P!, S!, UC).

Evergreen shrub or slender tree to ca. 2–9 meters tall, bark not seen. Twigs moderately angled, slender, moderately lepidote, otherwise glabrous to sparsely pubescent. Buds ovoid, 1–2 by 0.8–1.3 mm. Leaf blades elliptic to ovate, 3–7.3 by 1.2–3.6(–5.2) cm., ± flat, coriaceous, ca. 0.25–0.3 mm. thick; apex slightly acuminate or acute, to rounded or truncate; base narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to very obscurely toothed, proximal portion ± entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales usually quickly deciduous, with sparse to moderate pubescence on midvein, especially proximal portion, sometimes extending to secondary veins, the 3° and higher order veins usually visible, the 2° veins often clearly connected in series of arches, not depressed; abaxial surface moderately lepidote, otherwise densely pubescent, the 3° and higher order veins ± flat, slightly and laxly reticulate to obscure, the 2° veins usually visible and slightly raised; scales rust colored, becoming whitish with age, usually persistent, ca. 0.08–0.23 mm. in diameter, erose to nearly entire; petiole 4–6 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 5- to 10-flowered. Pedicels clearly articulated with calyx, slender, 4.5–7.5 mm. long, lepidote (scales light orange to whitish), otherwise glabrous to sparsely pubescent; bracteoles subopposite, basal or nearly so, narrowly triangular, 0.5–1.2 mm. long; bracts to ca. 2 mm. long. Flowers 4- (or 5-)merous; calyx lobes triangular, with acuminate apices, 1–1.7 by 0.6–1.3 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise usually sparsely pubescent near base; corolla ± cylindrical (to long-urceolate?), 4–5.5 by 2–3 mm., white, adaxially sparsely lepidote; filaments roughened, 2.5–3.5 mm. long, unappendaged or with minute spurs near anther-filament junction, anthers 0.6–1.1 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule long-ovoid with ± straight sides, (5–)6–7.5 by 1.5–3(–3.5) mm., sparsely lepidote, otherwise sparsely pubescent, especially near base, with pale, very thick sutures; seeds 2.5–3.5 mm. long. (FIGURE 48.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, near Santa Catalina (Monte Toro) and Monte Verde (MAP 26). Dense woods and thickets in mountains.

ADDITIONAL SPECIMENS EXAMINED. **Cuba.** ORIENTE: Farallones, Sta. Catalina in Monte Toro, 1 May [1861], *Wright 2197*, in part (GH, GOET, MO, NY, S).

Lyonia elliptica is poorly represented and has often been taxonomically misunderstood. Only two collections are known, and both of these are by Charles Wright (see below). There is very little information about its ecology, and even that given in the description above will probably be modified if the plant is ever studied in the field. *Lyonia elliptica* is probably closely related to *L. affinis*, from which it differs in its usually 4-merous flowers and in its narrower, long-ovoid capsules. It has sometimes been confused with *L. trinidadensis* (see discussion under this species).

In 1866 Grisebach listed "*L. elliptica* Wr. mscr." as a synonym of *Lyonia latifolia*, citing *Wright 2197*. Actually, this number of C. Wright is a mixed collection containing four elements: 1) specimens of *L. macrophylla* from a pinal near Baracoa collected on 15 June [1861]; 2) specimens of *L. macrophylla* from Pinal Mayari Abajo collected on 6 August [1860]; 3) a collection of *L. elliptica* with old flowers collected at Monte Verde on 18 July [1860 or 1861]; and 4) a collection of *L. elliptica* with mature capsules from Monte Toro near Sta. Catalina collected on 1 May [1861]. Nearly all of the specimens distributed under *Wright 2197* by Asa Gray lack this locality information, but the original labels (in Wright's handwriting) are present on the specimens at GH, and the information for the first element is repeated on the specimen at GOET. The years enclosed in brackets are not included on the field slips giving locality information but are those most in accord with C. Wright's itinerary (see Underwood, 1905). In 1914 Small took up Wright's manuscript name for his new species *Xolisma elliptica* and selected the third element as the type, a decision that probably was correct because with the specimen of this element at GH is a field label that states "Andromeda elliptica. A slender tree 30′± high in dense woods Monte Verde July 1." The original labels for the first, second, and fourth elements are, in contrast, not identified to species, giving only "Lyonia *not* jamaicensis ex descrip. . . . ," "Ericaceae . . . ," and "Lyonia . . . ," respectively. Unfortunately, Small's concept of this taxon was very broad, including also all of *L. trinidadensis* and part of *L. affinis*. On the fourth element of *Wright 2197* at GOET is written "A. (Lyonia) elliptica" in Asa Gray's handwriting, possibly indicating that Gray considered this collection to be conspecific with Wright's name, which was at that time still unpublished. The third and fourth elements appear, at first glance, to be rather different. The type of *L. elliptica* (i.e., the third element) has more acute or acuminate leaves, slightly more pubescent twigs, slightly longer pedicels, and a higher frequency of 5-merous flowers. However, these differences are not greater than those separating the types of *L. affinis* and *L. brittonii* or *L. myrsinifolia*, and it seems likely that additional collections will fill in the morphological gap between these two collections. Finally, it is interesting to note that no other lyonias have been collected at either Monte Toro or Monte Verde.

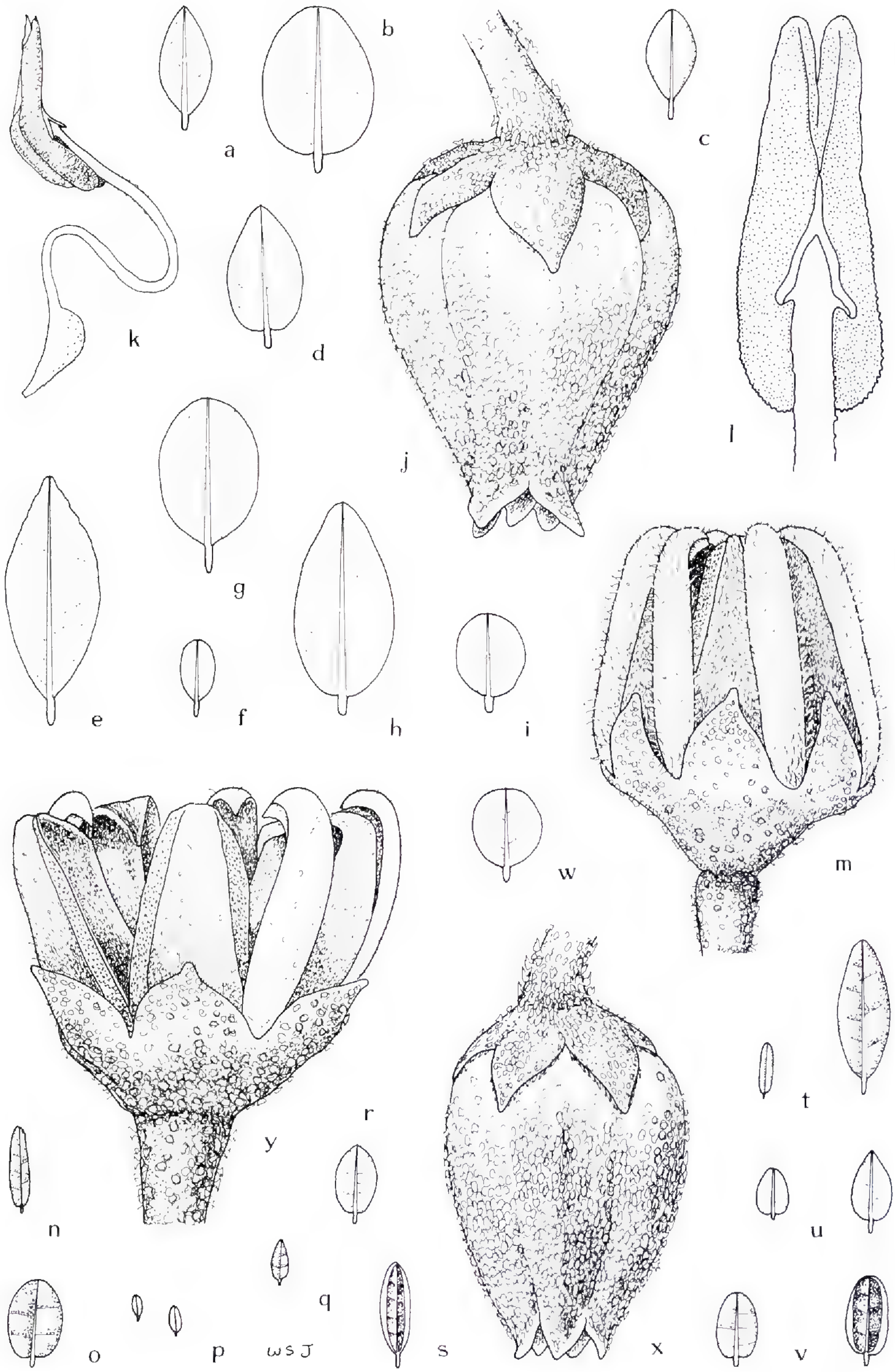
24. **Lyonia nipensis** Urban, Repert. Sp. Nov. **22:** 47. 1925. TYPE: Cuba, prov.

Oriente, Sierra de Nipe, near Río Piedra, 24 July 1914, *E. L. Ekman 2156* (holotype, S; isotypes, NY, S!).

Evergreen shrub to ca. 2 meters tall, with grayish(?), longitudinally furrowed bark. Twigs moderately angled, slender, sparsely to moderately lepidote, otherwise densely to sparsely pubescent. Buds ovoid, 0.7–1.8 by 0.5–1.1 mm. Leaf blades ovate to slightly obovate or nearly orbicular, 0.9–4.5(–6) by 0.4–3(–3.5) cm., ± flat or strongly recurved, often strongly coriaceous, ca. 0.35–0.55 mm. thick; apex rounded or truncate to obtuse or acute; base cuneate to rounded or slightly cordate; margin plane to very strongly revolute, distal portion entire to undulate, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, densely to sparsely pubescent on midvein, especially proximal portion, the 2° and higher order veins visible to obscure, the 2° veins slightly raised to strongly depressed; abaxial surface moderately lepidote, otherwise usually densely pubescent (rarely only sparsely pubescent near margin or apex), the 3° and higher order veins ± flat or nearly so, slightly and laxly reticulate to obscure, the 2° veins slightly raised to obscure; scales rust colored, often becoming whitish with age, deciduous or persistent, ca. 0.12–0.37 mm. in diameter, erose to entire, sometimes of 2 distinct types; petiole 1.5–7.5 mm. long, lepidote, otherwise pubescent all around or less commonly only adaxially. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 1- to 10-flowered. Pedicels clearly to only weakly articulated with calyx, slender, 4–15(–20) mm. long, lepidote (scales orange to deeply orange-red, or brownish), otherwise sparsely to densely pubescent; bracteoles subopposite to alternate, basal or nearly so, narrowly triangular, 0.4–1.5 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate to acute apices, 1–3(–4) by 0.8–2 mm., the adaxial side often sparsely lepidote near margins, otherwise sparsely pubescent, especially near apex, the abaxial side moderately to densely lepidote, otherwise glabrous to sparsely pubescent, especially near base; corolla long-urceolate, 3.5–8 by 3–4.7 mm., white to occasionally pinkish, especially toward mouth, abaxially ± densely lepidote, causing flowers to appear yellowish or golden; filaments roughened, 2–4 mm. long, usually with very short spurs near anther-filament junction, anthers 1–1.6 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid, usually with straight-sided valves, 4–9 by 4–7 mm., lepidote, otherwise sparsely to densely pubescent, especially near base or on sutures, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–2.7 mm. long.

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, in thickets, serpentine barrens, and open forests of *Pinus cubensis* in the Sierra de Nipe, Sierra de Cristal, Sierra de Moa, Sierra de Toa, on Monte Libano, and on plateau near Moa; ca. 300–1000 m. alt.

FIGURE 49. a–m, *Lyonia nipensis* var. *nipensis:* a–i, leaves, × .5; j, flower, × 6; k, stamen, × 12.5; l, anther (abaxial surface), × 25; m, capsule, × 6. n–y, *L. nipensis* var. *depressinerva:* n–w, leaves, × .5; x, flower, × 6; y, capsule, × 6.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Key to the Varieties of *Lyonia nipensis*

1. Leaf blades ± flat, the margins usually at most slightly revolute, the midvein not depressed, or only slightly depressed and secondary veins not depressed, the abaxial surface usually with 1 scale type (irregular margined and usually deciduous); petiole (2.5–)3–7.5 mm. long; [northern Oriente, from Sierra de Nipe to plateau near Moa] . . . 24a. var. *nipensis*.
1. Leaf blades strongly recurved, the margins often strongly revolute, the midvein and secondary veins depressed, often strongly so, the abaxial surface with 2 scale types (irregular margined and deciduous, and smaller, ± entire margined, and persistent); petiole 1.5–4 mm. long; [Sierra de Moa and Sierra de Toa] . . . . . 24b. var. *depressinerva*.

24a. **Lyonia nipensis** Urban var. **nipensis**

Lyonia libanensis Urban, Repert. Sp. Nov. **22:** 43. 1925. TYPE: Cuba, prov. Oriente, near Guantánamo, in Monte Libano toward San Fernandez, ca. 700 m. alt., 24 December 1919, *E. L. Ekman 10266* (holotype, S!; fragment of holotype, NY!).

Buds ovoid, 1–1.8 by 0.8–1.1 mm. Leaf blades elliptic to ovate or slightly obovate, 1.2–4.5(–6) by 0.8–3(–3.5) cm., ± flat; base cuneate to rounded or slightly cordate; margin plane to slightly revolute (rarely ± strongly revolute); adaxial surface with midvein ± flat or only slightly depressed, the 2° veins obscure to visible and flat, forming ± acute angle with midvein; abaxial surface usually densely pubescent (rarely only sparsely pubescent near margin or apex); scales usually ± erose, usually deciduous; petiole (2.5–)3–7.5 mm. long. Calyx lobes 1.6–3(–4) by 1–2 mm.; corolla 4.5–8 by 3–4.7 mm.; filaments 2.5–4 mm. long, anthers 1.2–1.6 mm. long. Capsule 4–9 by 4.5–7 mm. (FIGURES 44, 49.)

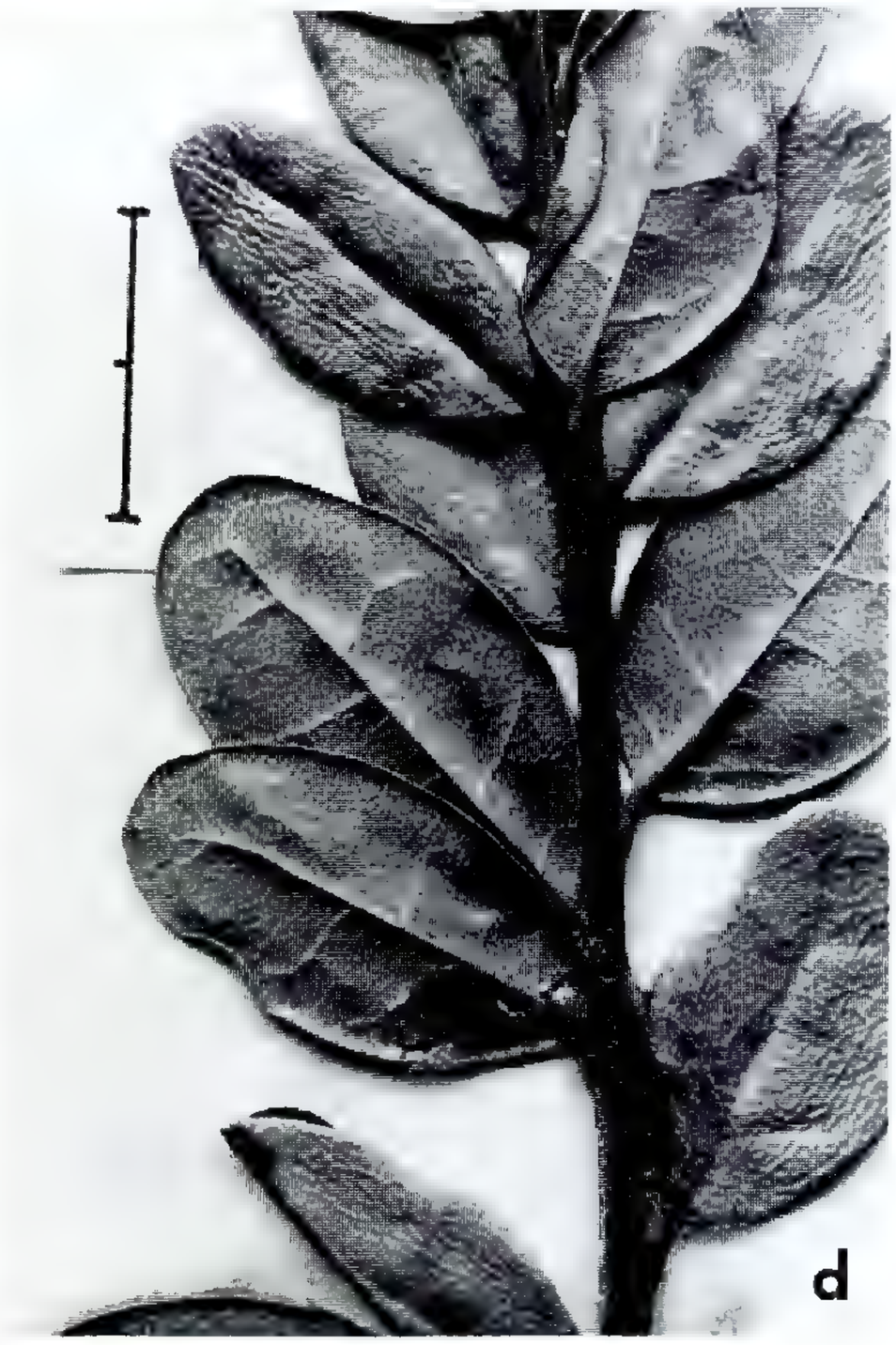
DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra de Nipe, Sierra de Cristal, on Monte Libano, and on plateau near Moa (MAP 25). Moist forests (''monte''), thickets (''charrascal''), and open forests of *Pinus cubensis* (''pinar''); ca. 300–1000 m. alt. Chiefly on reddish limonite soils (rich in iron, manganese, and nickel) derived from laterization of underlying serpentine rocks. The ''monte'' a moist forest of many trees growing so close that only small amount of light reaches forest floor; the ''charrascal'' a semi-xerophytic community mainly of woody shrubs and small trees often with small, coriaceous, revolute-margined leaves smooth and lustrous above and tomentose beneath (see Carabia, 1945; also Shafer, 1910; León, 1941, 1946;

FIGURE 50. a, *Lyonia nipensis* var. *depressinerva* (holotype, *Alain 3619*, NY): note small, strongly revolute leaves with depressed veins. b, *L. macrophylla* (*Clemente 3855*, GH): note twig densely covered with unicellular hairs, leaves lacking such hairs on abaxial surface. c, *L. obtusa* var. *longipes* (*Ekman 15973*, S): note clearly visible and reticulate tertiary veins on abaxial leaf surface. d, *L. obtusa* var. *obtusa* (isotype, *Wright 2203*, K): note obscure tertiary veins on abaxial leaf surface. Scale = 2 cm.

a

b

c


d

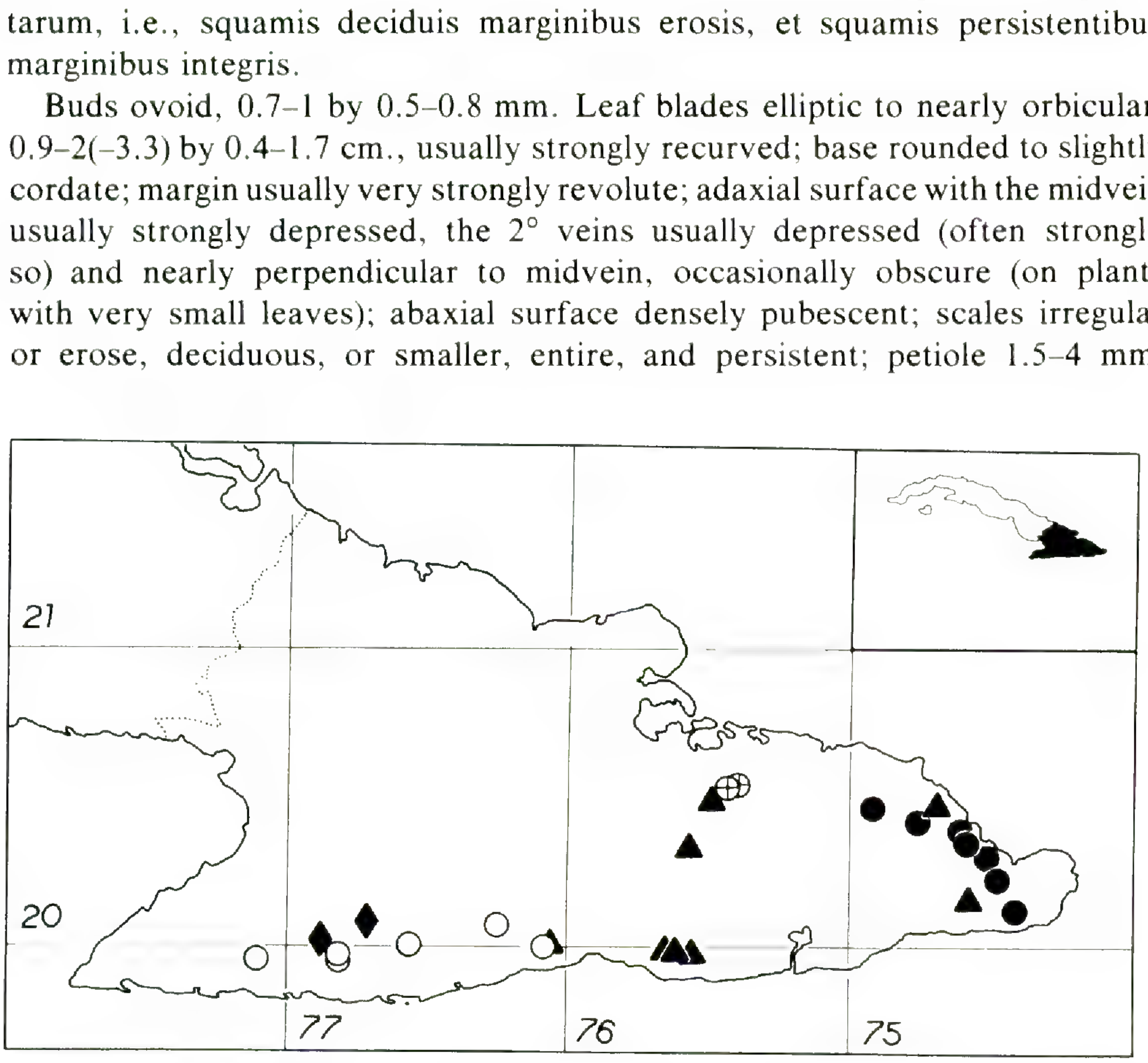
Smith, 1945; Alain, 1946a; and Marie-Victorin, 1956). Flowering mainly February through May.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Sierra de Cristal, Mayarí, "El Serrucho," *Bro. Alain et al. 5399* (GH); Sierra de Nipe, Cayo del Ray, Pinar Colorado, *Carabia 3576* (NY); Sierra de Nipe, Río Piloto, *Ekman 19153* (K, NY, S, US); Cerro Miraflores, Cananova, *Bros. León & Alain 19109* (GH, US); Sierra de Nipe, Cayo la Plancha, *Bro. León et al. 20017* (GH, US); Sierra de Nipe, near El Gurugú, *López-Figueiras 2579* (US); Moa, plateau between Río Cabanas and Río Moa, *Bro. Marie-Victorin 21736* (US); crest of Sierra de Nipe, *Morton & Acuña 3049* (UC, US); Loma Mensura, *Shafer 3789* (NY, US).

24b. **Lyonia nipensis** Urban var. **depressinerva** Judd, var. nov.

Varietas haec ab Lyonia nipensi Urban var. nipensi differt foliis minoribus, 0.9–2(–3.3) cm. longis, 0.4–1.7 cm. latis, ellipticis vel fere orbicularibus, nervo primario et nervis secundariis plerumque depressis, marginibus valde revolutis et petiolis brevioribus, 1.5–4 mm. longis, et typis duobus squamarum peltatarum, i.e., squamis deciduis marginibus erosis, et squamis persistentibus marginibus integris.

Buds ovoid, 0.7–1 by 0.5–0.8 mm. Leaf blades elliptic to nearly orbicular, 0.9–2(–3.3) by 0.4–1.7 cm., usually strongly recurved; base rounded to slightly cordate; margin usually very strongly revolute; adaxial surface with the midvein usually strongly depressed, the 2° veins usually depressed (often strongly so) and nearly perpendicular to midvein, occasionally obscure (on plants with very small leaves); abaxial surface densely pubescent; scales irregular or erose, deciduous, or smaller, entire, and persistent; petiole 1.5–4 mm.



MAP 27. Distribution of *Lyonia obtusa* var. *obtusa* (dots), *L. obtusa* var. *longipes* (circles with cross), *L. latifolia* var. *latifolia* (circles), *L. latifolia* var. *calycosa* (triangles), and *L. maestrensis* (diamonds).

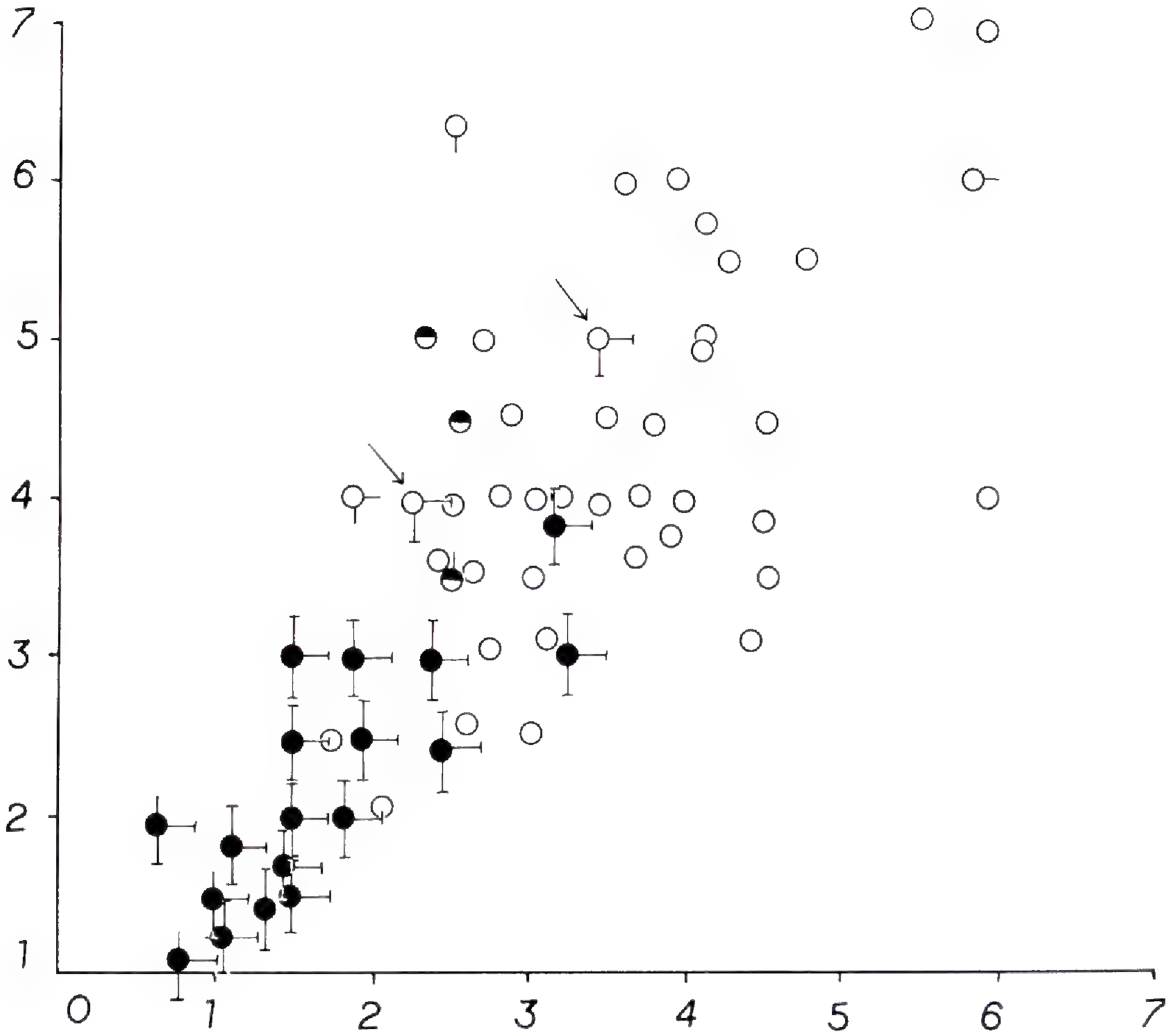


FIGURE 51. Scatter diagram showing variation between *Lyonia nipensis* var. *nipensis* and var. *depressinerva* in seven characters. Vertical axis = petiole length in mm.; horizontal axis = leaf length in cm.; closed circle = leaf blade curved toward abaxial surface, open circle = leaf blade ± flat, half-closed circle = intermediate; full tail to right = peltate scales of two kinds, no tail to right = peltate scales of one kind, half tail to right = intermediate; full tail up = leaf veins clearly depressed (at least midvein), half tail up = midvein slightly depressed, no tail up = leaf veins not depressed; full tail down = Sierra de Moa and Sierra de Toa populations, half tail down = Moa plateau, no tail down = Sierra de Nipe, Sierra de Cristal, and Monte Libano. Arrows indicate intermediate plants.

long; calyx lobes 1–2 by 0.8–1.1 mm.; corolla 3.5–5.5 by ca. 3 mm.; filaments 2–3 mm. long, anthers 1–1.3 mm. long. Capsule 4–5.5 by 4–5 mm. (FIGURES 49, 50.)

TYPE: Cuba, prov. Oriente, serpentine barrens, Peña Prieta, La Magdalena, Toa, 30 December 1953, *Bro. Alain 3619* (holotype, NY!; isotype, GH!).

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra de Moa and Sierra de Toa (MAP 25). Thickets, serpentine barrens, and open forests of *Pinus cubensis;* ca. 450–900 m. alt.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Peña Prieta, Toa, *Bro. Alain 3198* (GH); Sierra de Moa, *Bro. Alain 3412* (GH), *3422* (GH); trail from Camp La Barga to Camp San Benito, *Schafer 4115* (NY); Camp La Gloria, S. of Sierra de Moa, *Shafer 8263* (NY).

Lyonia nipensis is very closely related to *L. obtusa*, from which it is readily distinguished by the dense covering of unicellular hairs on its abaxial leaf surfaces and by its more or less erose, ferrugineous scales. These two species are essentially geographically isolated (MAPS 25, 27), and in the few localities where they overlap no intermediates have been seen.

Lyonia nipensis var. *nipensis* can be distinguished from var. *depressinerva* by its leaves that have blades more or less flat, margins flat to only slightly revolute, midvein at most only slightly depressed, secondary veins never depressed, and petioles longer (see FIGURES 44, 50, 51). In addition, the ferrugineous scales of the abaxial leaf surface are all more or less irregular and deciduous.

The characteristic that allows var. *depressinerva* to be recognized immediately is the striking aspect of its leaves. They are very small, with strongly revolute margins, and with the midvein and often the secondary veins depressed, frequently strongly so. The effect is enhanced by the tendency of the secondary veins to diverge from the midvein at an angle of nearly 90°. The epithet *depressinerva* is derived from this very characteristic venation. This variety also has very short petioles and two distinct types of peltate scales on its abaxial leaf surfaces (see FIGURES 50, 51).

The two varieties are more or less geographically isolated (MAP 25); however, *Alain 3446* (collected in the Sierra de Moa at 900 meters) is intermediate. It has the flat leaves with midvein and secondary veins not depressed and the quite long petioles of var. *nipensis*, but the two distinct types of peltate scales of var. *depressinerva*. More field work is needed to determine the extent of intergradation between the two taxa.

Plants of var. *nipensis* from the limonite plateau near Moa often have slightly smaller, less erose, and more persistent scales than do populations of the Sierra de Nipe. The single collection from Monte Libano has more acute leaves than is usual in populations of the Sierra de Nipe, but occasional acute-leaved specimens (e.g., *León & Alain 19109*) have been collected there, and this character, quite variable in most species, would be an exceedingly poor basis on which to segregate the Monte Libano plant as a third variety.

25. **Lyonia obtusa** Griseb. Catal. Pl. Cubens. 51. 1866.

Evergreen low shrub to small tree to ca. 5 meters tall, with grayish to brownish, longitudinally furrowed bark. Twigs moderately to slightly angled, slender, sparsely lepidote, otherwise densely to sparsely pubescent. Buds ovoid, 0.8–1 by 0.6–1 mm. Leaf blades elliptic, widely elliptic, obovate, or ovate, 0.8–7.6 by 0.6–6 cm., flat to strongly recurved, often strongly coriaceous, ca. 0.45–0.56 mm. thick; apex acute to rounded to truncate; base broadly cuneate to slightly cordate; margin plane to strongly revolute, distal portion entire to undulate or occasionally very obscurely toothed, proximal portion

entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales usually quickly deciduous, sparsely pubescent on proximal portion of midvein, 3° and higher order veins visible to less commonly obscure, midvein sometimes depressed, 2° veins visible and flat to strongly depressed; abaxial surface sparsely lepidote, otherwise glabrous, sometimes very sparsely pubescent on midvein near petiole (but not on lamina surface), the 3° and higher order veins ± flat to very slightly raised, laxly reticulate, the 2° veins raised and visible; scales rust colored, persistent to deciduous, ca. 0.12–0.17 mm. in diameter, ± entire; petiole 1.5–9 mm. long, lepidote, otherwise pubescent all around or less commonly only adaxially. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 1- to 8-flowered. Pedicels clearly to only weakly articulated with calyx, slender, 8–31 mm. long, lepidote, otherwise sparsely to densely pubescent; bracteoles subopposite to alternate, near base of pedicel, narrowly triangular, 0.5–1.5 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate to acute apices, 1.3–3 by 0.7–1.7 mm., the adaxial side often sparsely lepidote near margins, otherwise sparsely pubescent, especially near apex, the abaxial side lepidote, sometimes densely so, otherwise glabrous to moderately pubescent near base; corolla long-urceolate, 5–7 by 3.5–4.7 mm., white to pink, occasionally reddish toward mouth, abaxially moderately to densely lepidote, the flowers thus appearing golden; filaments roughened, 2.7–4 mm. long, usually with very short spurs to ca. 0.1 mm. long near anther-filament junction, anthers 0.8–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid, usually with straight-sided valves, 4–9 by 3.5–6.5 mm., lepidote, otherwise sparsely to densely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.5–2.5 mm. long.

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente; thickets, rocky slopes, and forests of *Pinus cubensis;* mountains south and west of Baracoa, Sierra de Toa, and Sierra de Cristal; ca. 350(?)–1300 m. alt.

Key to the Varieties of *Lyonia obtusa*

1. Leaves to ca. 7 cm. long, usually slightly to strongly recurved, often with midvein and/or secondary veins depressed, the abaxial side with tertiary veins much less prominent than secondary, obscure to slightly reticulate; apex usually rounded; [Moa-Baracoa region] . . . . . 25a. var. *obtusa.*

1. Leaves to ca. 3.5 cm. long, flat, veins not depressed, the abaxial side with tertiary veins nearly as prominent as secondary, forming a strong reticulate pattern; apex acute to rounded; [Sierra de Cristal] . . . . . 25b. var. *longipes.*

25a. **Lyonia obtusa** Griseb. var. **obtusa**

Andromeda obtusa (Griseb.) C. Wright in Sauvalle, Anal. Acad. Ci. Habana **6:** 250. 1870. *Xolisma obtusa* (Griseb.) Small, N. Am. Fl. **29**(1): 69.

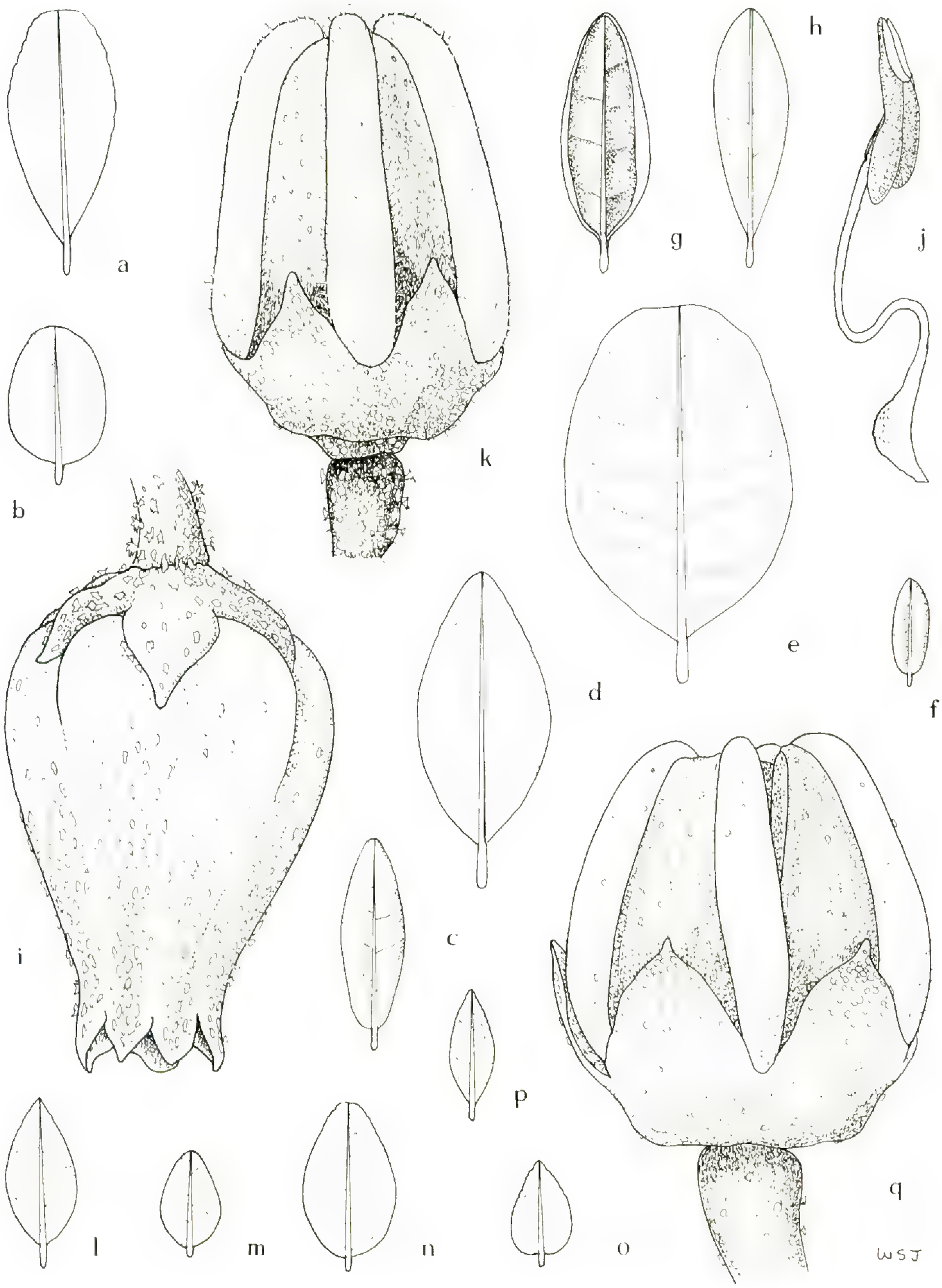


FIGURE 52. a–k, *Lyonia obtusa* var. *obtusa:* a–h, leaves, × .5; i, flower, × 6; j, stamen, × 12.5; k, capsule, × 6. l–q, *L. obtusa* var. *longipes:* l–p, leaves, × .5; q, capsule, × 6.

1914. TYPE: Cuba, [prov. Oriente], Cuchillas de Baracoa, 21 June [1861], *C. Wright 2203* (holotype, GOET!; isotypes, GH!, K!, P!; fragments of isotypes, L!, NY!).

Lyonia oblongata Urban, Repert. Sp. Nov. **22:** 47. 1925. TYPE: Cuba, prov. Oriente, near Baracoa in carrascales along Río Joa [Toa], 1914, *E. L. Ekman 3678* (holotype, s!; isotype, NY!).

Shrub to small tree to ca. 5 meters tall. Twigs densely to sparsely pubescent. Leaf blades elliptic, widely elliptic, to obovate or ovate, 1.2–7.6 by 0.6–6 cm., flat to slightly or strongly recurved; apex rounded or truncate; base broadly cuneate to rounded; margin slightly to strongly revolute; adaxial surface with midvein and often 2° veins usually slightly to strongly depressed; abaxial surface with the 3° and higher order veins obscure to slightly and laxly reticulate, much less prominent than 2° veins; petiole 2–9 mm. long. Pedicels 3–25 mm. long, clearly to only weakly articulated with calyx. Calyx lobes 1.3–2.5(–3) mm. long. Capsule 4.5–9 by 3.5–6.5 mm., moderately to densely pubescent. (FIGURES 50, 52.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, mountains south and west of Baracoa and Sierra de Toa (MAP 27). Thickets and forests of *Pinus cubensis* on reddish, deep, lateritic soils; ca. 350(?)–900(?) m. alt. (Pine forests near Baracoa briefly described by León (1946) and Smith (1954).) Flowering December to June.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Pinares de Sabanilla, Baracoa, *Acuña & Barreto 17476* (NY); near Baracoa toward Mayarí, *Ekman 4022* (S); Mesa de Prada, Jauco, S. Baracoa region, *Bro. León 11972* (GH, NY); trail from Camp La Barga to Camp San Benito, *Shafer 4103* (NY); Camp La Gloria, S. of Sierra de Moa, *Shafer 8211* (NY).

25b. **Lyonia obtusa** Griseb. var. **longipes** (Urban) Judd, comb. et stat. nov.

Lyonia longipes Urban, Repert. Sp. Nov. **18:** 22. 1922. TYPE: Cuba, prov. Oriente, near summit of Sierra de Cristal, 1200–1300 m. alt., 8 March 1916, *E. L. Ekman 6824* (holotype, s!; fragment of holotype, NY!).

Low shrub. Twigs sparsely pubescent. Leaf blades ovate to elliptic, 1–3.5 by 0.7–2.3 cm., ± flat; apex acute to rounded; base rounded to slightly cordate; margin plane to slightly revolute; adaxial surface with midvein and 2° veins not depressed; abaxial surface with the 3° and higher order veins slightly and laxly reticulate, as prominent as 2° veins (or nearly so); petiole 1.5–5 mm. long. Pedicels 9–31 mm. long, usually clearly articulated with calyx. Calyx lobes 2–3 mm. long. Capsule 4–7 by 4–6 mm., sparsely pubescent. (FIGURES 50, 52.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra de Cristal (MAP 27). Dense thickets, dwarfed *Pinus cubensis* forests(?), rocky slopes, or with *Arthrostilidium;* ca. 600–1300 m. alt. (Vegetation of this mountain range briefly described in Alain (1956).)

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Sierra de Cristal, near summit of El Cristal, Mayarí, *Bro. Alain et al. 5702* (GH); Río Lebisa, *Ekman 15943* (S, NY).

Lyonia obtusa is readily distinguished from its close relative, *L. nipensis*, by the lack of unicellular hairs covering the abaxial surface of its leaf blades and by its ± entire-margined, ferrugineous scales. These two taxa are remarkably similar in most other respects, both having robust, ovoid capsules with straight-sided valves and often elongated pedicels, and both exhibiting marked variation in leaf size and shape, degree of depression of primary and secondary veins, and extent of marginal revolution (FIGURES 49, 52).

Lyonia obtusa var. *longipes* can readily be distinguished from var. *obtusa* by its smaller, fairly flat leaves with acute to rounded apices and more or less clearly reticulate, not depressed veins (see key). (Since this taxon differs from var. *obtusa* only in a few vegetative characters, Urban's *Lyonia longipes* (1922) is here reduced to a variety of *L. obtusa*.) Variety *longipes* is endemic to the Sierra de Cristal and is thus geographically isolated from var. *obtusa* (MAP 27).

26. **Lyonia macrophylla** (Britton) Ekman ex Urban, Repert. Sp. Nov. **22:** 42. 1925.

Xolisma macrophylla Britton in Small, N. Am. Fl. **29**(1): 70. 1914. TYPE: Cuba, prov. Oriente, SE. of Paso Estancia, 1–2 May 1909, *Shafer 1680* (holotype, NY!; isotypes, HAC?, NY (2 sheets)!).

Lyonia brachytricha Urban, Repert. Sp. Nov. **18:** 21. 1922. TYPE: Cuba, prov. Oriente, near Baracoa, toward Florida, 18 Nov. 1914, *E. L. Ekman 3502* (holotype, S!; fragment of holotype, NY!).

Evergreen shrub or small tree to ca. 6 meters tall, with grayish or brownish(?), longitudinally furrowed bark. Twigs moderately to slightly angled, slender, moderately lepidote, otherwise densely pubescent. Buds ovoid, 1–2 by 0.8–1.6 mm. Leaf blades elliptic to widely elliptic, obovate, or ovate, 2–7(–8.5) by 1.2–4(–5.5) cm., ± flat, coriaceous, ca. 0.3–0.37 mm. thick; apex usually rounded or truncate, occasionally acute or obtuse; base attenuate or narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to very obscurely and irregularly toothed, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales usually quickly deciduous, densely pubescent on midvein, especially proximal portion, often sparsely pubescent on 2° and some 3° veins, the 3° and higher order veins visible, the 2° veins slightly raised, with interconnections usually clearly evident; abaxial surface moderately lepidote, otherwise glabrous, often very sparsely pubescent on proximal portion of midvein and rarely on some 2° veins (but not on lamina surface), the 3° and higher order veins flat or nearly so, slightly and laxly reticulate, the 2° veins raised and visible; scales rust colored, usually persistent, ca. 0.07–0.2 mm. in diameter, entire to erose; petiole 4–17 mm. long, lepidote, otherwise pubescent all around. Flower buds

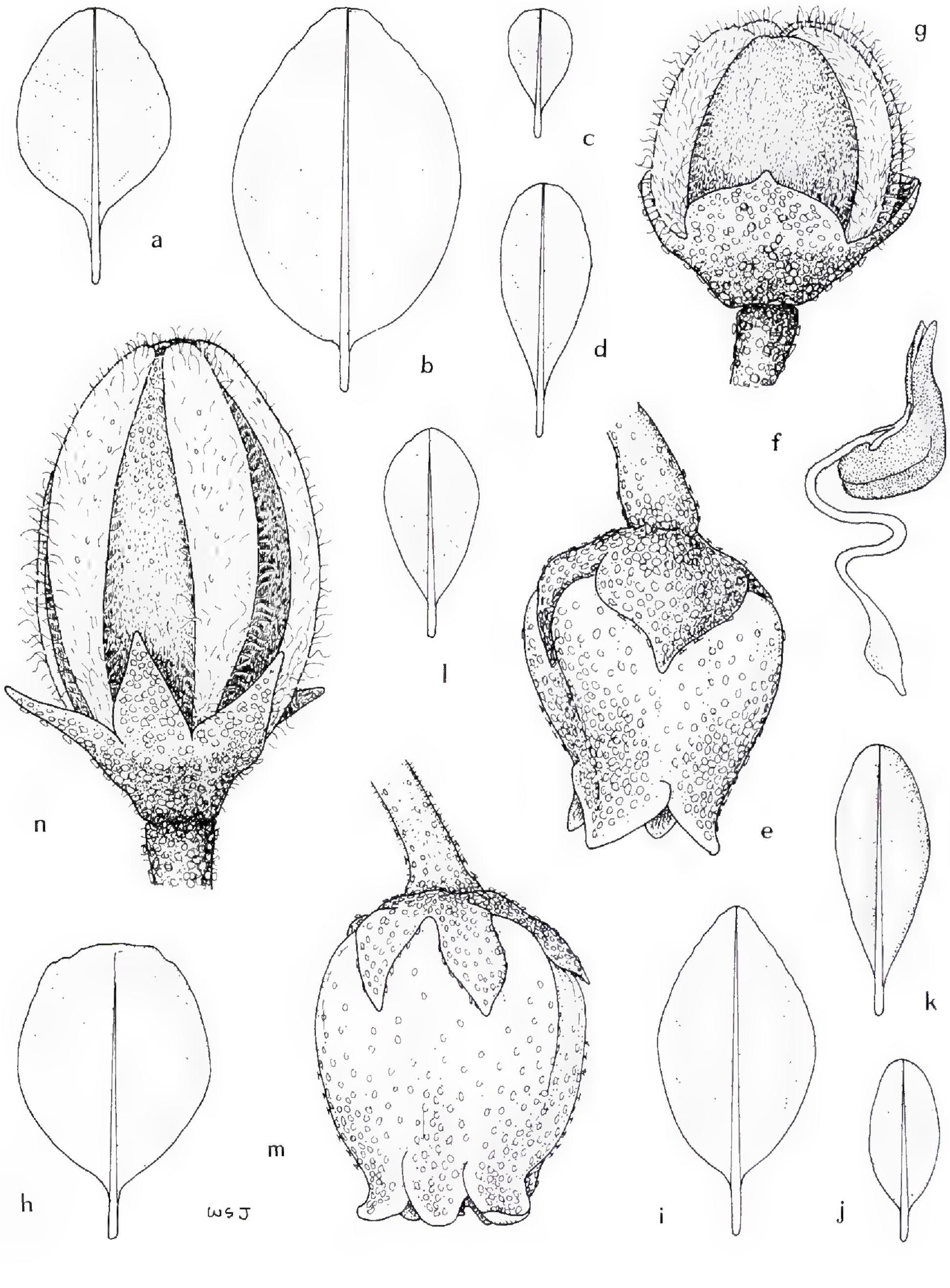


FIGURE 53. a–g, *Lyonia ekmanii:* a–d, leaves, × .5; e, flower, × 6; f, stamen, × 12.5; g, capsule, × 6. h–n, *L. macrophylla:* h–l, leaves, × .5; m, flower, × 6; n, capsule, × 6.

above or intermixed with vegetative buds; inflorescences fasciculate (or rarely shortly racemose), 4- to 15-flowered. Pedicels clearly to only weakly articulated with calyx, slender, 5–12 mm. long, lepidote, otherwise sparsely to densely pubescent; bracteoles subopposite to alternate, nearly basal, narrowly triangular, 0.5–1.4 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate to acute apices, 1.4–2.5 by 0.8–1.5 mm., the adaxial side glabrous to densely pubescent, especially near apex, the abaxial side lepidote, otherwise usually sparsely to moderately pubescent, especially near base, corolla long-urceolate, 4.5–7 by 2.5–4 mm., white to occasionally pink tinged, abaxially moderately to occasionally densely lepidote, and rarely otherwise very sparsely pubescent; filaments roughened, 2.5–4 mm. long, usually with pair of spurs to ca. 0.13 mm. long just below anther-filament junction, anthers ca. 1–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to ellipsoid, with ± convex valves, 4.5–8.5 by 3.5–5 mm., lepidote, otherwise densely to moderately pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–3.5 mm. long. (FIGURES 50, 53; see also Roig & Acuña in León & Alain (1957).)

DISTRIBUTION AND ECOLOGY. Cuba, mountains of northern Oriente prov. from Sierra de Nipe to Moa-Baracoa region (MAP 26). Thickets, rocky areas, wooded stream banks, forests of *Pinus cubensis;* on reddish, lateritic soil; to ca. 850 m. alt. See Borhidi (1979) for list of characteristic species of these forests. Vegetation of Moa region briefly described by León (1941), Marie-Victorin (1942), Seifriz (1943), and Alain (1946a). Marie-Victorin (1944) included photo of *Pinus cubensis* forest. Carabia (1945) listed *L. macrophylla* as a species of exposed areas in the *Jacaranda arborea–Tabebuia pachyphylla–Cecropia peltata* community along streams in Sierra de Nipe. Flowering chiefly June through August.

COMMON NAME. Sangre de toro (Roig, 1965).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: vic. of Moa, airport, *Acuña 12648* (US); vicinity of Moa, Playa Vaca, *Acuña 12649* (US); Sierra de Moa, near Cayo Fortuna, *Bro. Alain 3293* (GH); Sierra de Mícara, Mayarí, *Bro. Alain et al. 4852* (GH, IJ, US); Sierra de Nipe, Pinar Colorado, Cayo Rey, *Bro. Alain et al. 4834* (GH); 17 km. S. of Baracoa, *Bro. Alain & Morton 5112* (GH); Cañete, *Aubelo s.n.*, 2 Jan. 1952 (NY); Cayo, Chiquito, Moa, *Bros. Clemente & Alain 3804* (GH, US); Río Yagrumajes, Moa, *Bro. Clemente 3836* (GH); Sierra de Nipe, Río Piedra, *Ekman 1823* (S); Lomas de Cuaba, near Baracoa, *Ekman 4231* (S); Sierra de Nipe, Loma Mensura, *Ekman 9702* (K, NY, S); Sierra de Mícara, *Ekman 16024* (S); Sierra de Nipe, Río Piloto, *Ekman 19154* (NY, S); 15 km. SW. of Compania de Moa mill, foothills of Sierra de Moa, *Howard 6035* (GH, NY); Sierra de Nipe, Mayarí, near Sojo cascade, *Bros. León & Alain 17970* (GH); Sierra de Nipe, S. of La Mensura, *Bros. León & Alain 19923* (US); near Punta Gorda, Moa, *Bro. León et al. 20818* (GH); Cerro de Miraflores, Cananova, *Bro. León 21125* (GH, US); Moa, *Bro. León et al. 22503* (GH); between Los Mulos and La Corea, below Sierra del Cristal, *López-Figueiras 219* (NY, US); Sierra de Nipe, near source of

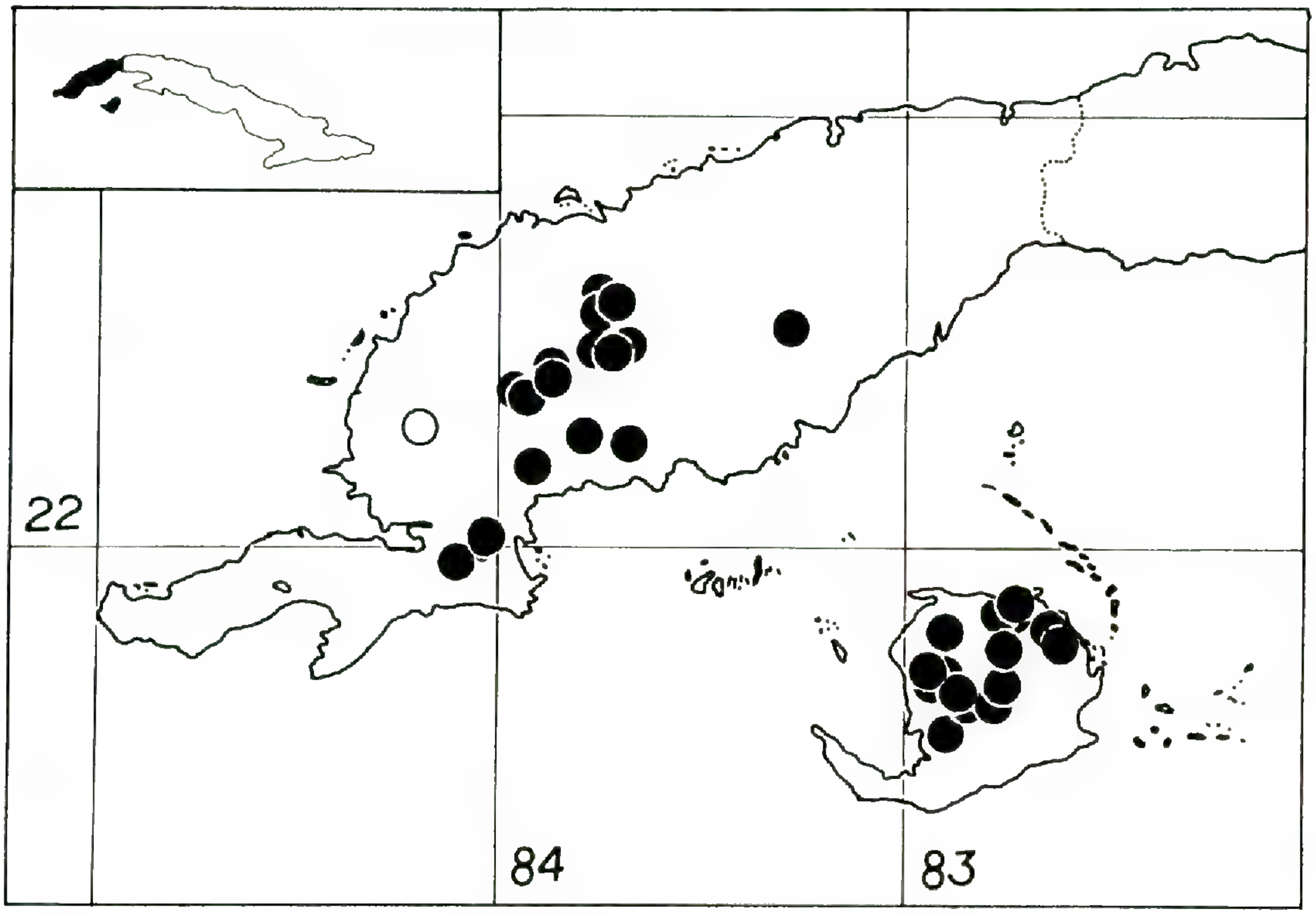
Arroyo Pinarito, *López-Figueiras 2589* (US); between Sabanilla and Cajobabo on Via Azul, at km. 7 from Sabanilla, *Morton & Bro. Alain 9090* (US); Pinar de El Purio, Cabonico, *Roig 142* (NY); Sierra de Nipe, near Woodfred, *Shafer 2996* (NY, US); Río Naranja, about the falls, *Shafer 3866* (NY); Moa region, serpentine platform, ca. 20°41′N., 74°56′W., *Webster 3854* (GH, US); Pinal Mayarí abajo, *Wright 2197*, in part, 6 Aug. [1860] (GH, MO, NY, P, L); Pinal near Baracoa, *Wright 2197*, in part, 15 June [1861] (GH, GOET, L, MO, NY, P, S).

This species is probably most closely related to *Lyonia ekmanii*, a Pinar del Río endemic, from which it differs in its mainly five-merous flowers, its longer capsules, and its densely pubescent twigs. *Lyonia macrophylla* is also similar to *L. obtusa* but is easily differentiated by its capsules with convex valves, its often shorter pedicels, and its leaves that are moderately lepidote beneath and often have longer petioles. It has sometimes been confused with *L. affinis*, a species of the Sierra Maestra, which has more cylindrical, more sparsely lepidote corollas, and leaves that are usually abaxially densely pubescent.

Although this species is one of the most widespread and common lyonias of eastern Cuba, it is not separable into a series of locally differentiated populations and is more uniform than most other widespread species of Oriente. There is a slight tendency for plants of the Sierra de Nipe to have smaller, or at least narrower, leaves and shorter petioles, but many plants from this area are not distinguishable from those of the Moa-Baracoa region.

27. **Lyonia ekmanii** Urban, Repert. Sp. Nov. **22:** 45. 1925. TYPE: Cuba, prov. Pinar del Río, Arroyo Mantua, Damuji to Rincon del Prado, 21 May 1920, *E. L. Ekman 11026* (holotype, s!; isotypes, NY!, s!).

Evergreen shrub with longitudinally furrowed bark. Twigs moderately to slightly angled, slender, sparsely to moderately lepidote, otherwise glabrous to very sparsely pubescent. Buds ovoid, 1–2 by 1–1.3 mm. Leaf blades elliptic to widely elliptic, obovate, or ovate, 2–9 by 1.3–6 cm., ± flat, coriaceous, ca. 0.4–0.57 mm. thick; apex rounded to truncate; base attenuate, narrowly cuneate to rounded; margin plane to slightly revolute, distal portion entire to undulate, proximal portion ± entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales quickly deciduous, densely pubescent on midvein, especially proximal portion, sometimes sparsely pubescent on 2° veins, with 3° and higher order veins visible, 2° veins visible and slightly raised; abaxial surface moderately lepidote, otherwise glabrous, the 3° and higher order veins ± flat or nearly so, slightly and laxly reticulate, the 2° veins raised and visible; scales rust colored, usually persistent, ca. 0.14–0.25 mm. in diameter, entire to irregular; petiole 5–18 mm. long, lepidote, otherwise pubescent adaxially to nearly all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate or rarely shortly racemose, 1- to 11-flowered. Pedicels clearly to only weakly articulated with calyx, slender, 4–8 mm. long, lepidote, otherwise sparsely pubescent to



MAP 28. Distribution of *Lyonia ekmanii* (circle) and *L. myrtilloides* (dots).

glabrous; bracteoles subopposite, near base of pedicel, narrowly triangular, 0.8–3 mm. long; bracts to ca. 3 mm. long. Flowers 4- (or 5-)merous; calyx lobes triangular, with acuminate apices, 1.6–2.6 by 1.5–2.5 mm., the adaxial side glabrous to very sparsely pubescent toward apex, the abaxial side lepidote, otherwise glabrous to sparsely pubescent, especially near base; corolla urceolate to long-urceolate, 4–5 by 3–4 mm., white, abaxially ± moderately lepidote; filaments roughened, 2.5–3 mm. long, usually with pair of short spurs just below anther-filament junction, anthers 1.2–1.8 mm. long; Ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to globose or subglobose, usually with ± convex valves, 3.5–5 by 3.5–4.6 mm., lepidote, otherwise densely to moderately pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 3–3.5 mm. long. (FIGURE 53.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Pinar del Río (MAP 28). Sandy area; known only from type locality.

Lyonia ekmanii is closely related to *Lyonia macrophylla*, from which it differs in its mainly four-merous flowers with slightly wider calyx lobes, shorter corollas, and shorter capsules, and its essentially glabrous twigs lacking unicellular hairs. In addition, the leaves of *L. ekmanii* have a lignified hypodermis that those of *L. macrophylla* usually lack. The two species also differ ecologically, since *L. ekmanii* has been collected only in sandy soil, while *L. macrophylla* grows on red, lateritic soil. The close relationship of

these taxa was recognized by Urban (1925) when he described *L. ekmanii*. He stated, "affinis *L. brachytrichae* [= *L. macrophylla*] Urb., que ramis breviter pilosis, foliis brevius petiolatus, floribus 5-meris, corolla longiore differt." Of the differences cited by Urban, only that of petiole length has not proved useful when greater numbers of specimens were examined. *Lyonia ekmanii* and *L. macrophylla* are geographically isolated, the former occurring in Pinar del Río and the latter in Oriente.

Lyonia ekmanii is probably also related to *L. myrtilloides*, from which it is easily differentiated by its larger leaves, its more sparsely pubescent twigs, its wider capsules, its larger corollas, and its longer calyx lobes. Both taxa occur in the vegetation of the siliceous soils of Pinar del Río, and they may occur together.

28. **Lyonia myrtilloides** Griseb. Catal. Pl. Cubens. 51. 1866.

Lyonia myrtilloides Griseb. var. α *parvifolia* Griseb. (= var. *myrtilloides;* see discussion in text), Catal. Pl. Cubens. 51. 1866. *Xolisma myrtilloides* (Griseb.) Small, N. Am. Fl. **29**(1): 67. 1914. TYPE: Cuba, [prov. Pinar del Río], Pinar del Río–Viñales, 23 January [1864], 1 March [1864], November [1863?], *C. Wright 2195* (lectotype, GOET! = holotype of *L. myrtilloides* var. *parvifolia;* isotypes, GH (2 sheets)!, MO!, NY (3 sheets)!, P!, S (2 sheets)!, UC!, US!; fragment of isotype, L!).

Lyonia myrtilloides Griseb. var. β *ovalifolia* Griseb. Catal. Pl. Cubens. 51. 1866. *Andromeda glandulosa* (A. Rich.) C. Wright var. *ovalifolia* (Griseb.) Gómez de la Maza, Anal. Hist. Nat. Madrid **19:** 250. 1890. TYPE: Cuba, [prov. Pinar del Río], Los Cayos–Isabel Maria, 13 March [1864], *C. Wright 2196* (holotype, GOET!; isotypes, GH!, MO!).

Xolisma vaccinioides Small, N. Am. Fl. **29**(1): 68. 1914. *Lyonia vaccinioides* (Small) Acuña & Roig, Contr. Ocas. Mus. Hist. Nat. Col. La Salle **15:** 5. 1956. TYPE: Cuba, Isla de Pinos, Nueva Gerona, March 1904, *A. H. Curtiss* (holotype, NY!).

Evergreen shrub or small tree to 3(–6) meters tall, sometimes with strongly ascending branches, with longitudinally furrowed bark. Twigs moderately angled, slender, sparsely to densely lepidote, otherwise densely to occasionally moderately pubescent. Buds ovoid, 0.5–1.5 by 0.5–1 mm. Leaf blades narrowly to widely obovate or elliptic, or occasionally slightly ovate or orbicular, 0.7–4(–4.5) by 0.3–2(–3.1) cm., flat to slightly recurved, coriaceous, ca. 0.3–0.36 mm. thick; apex rounded to truncate; base attenuate, narrowly to broadly cuneate or rounded; margin plane to revolute, distal portion entire to undulate or occasionally very obscurely and irregularly toothed, proximal portion entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales quickly deciduous, densely to moderately pubescent on proximal portion of midvein, the 3° and higher order veins obscure to visible, the midvein ± flat or less commonly slightly depressed, the 2° veins visible and slightly raised to obscure, only rarely slightly depressed; abaxial surface sparsely to moderately lepidote, otherwise glabrous, often very sparsely pubescent on midvein, especially proximal portion (but not on lamina surface), the

3° and higher order veins ± flat or nearly so, slightly and laxly reticulate to obscure, the 2° veins raised and visible to obscure, irregular; scales rust colored, becoming whitish with age, usually persistent, ca. 0.09–0.26 mm. in diameter, entire to erose; petiole 1.5–5.5 mm. long, lepidote, otherwise pubescent ± all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, 1- to 10-flowered. Pedicels clearly to only weakly articulated with calyx, slender, 2.5–11 mm. long, lepidote, otherwise very sparsely to moderately pubescent; bracteoles subopposite, nearly basal, narrowly triangular, 0.4–1.2 mm. long; bracts to ca. 1.5 mm. long. Flowers 4- (or 5-)merous; calyx lobes triangular, with acuminate to nearly acute apices, 0.7–1.5 by 0.5–1.3 mm., the adaxial side sparsely pubescent, especially near apex, the abaxial side lepidote, otherwise glabrous or very sparsely pubescent near base; corolla urceolate to cylindrical, 2.5–4 by 1.7–2.7 mm., white, abaxially sparsely lepidote; filaments roughened, 1.3–2.3 mm. long, usually with 2 spurs to ca. 0.1 mm. long just below anther-filament junction, anthers 0.7–1.2 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule narrowly ovoid, straight sided, 3–4 by 1.7–3(–3.5) mm., lepidote, otherwise densely to moderately pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.5–2.5 mm. long. (FIGURE 54; see also Marie-Victorin & León (1944).)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Pinar del Río (including Isle of Pines) (MAP 28). White sand or gravel savannas (of *Colpothrinax wrightii, Acoelorraphe wrightii, Pinus* spp.), open pinelands (of *Pinus tropicalis* and *P. caribaea*), and thickets; to ca. 300 m. alt. Flora of these savannas and pinelands discussed (with lists of characteristic species) in Jennings (1917), Seifriz (1943), Marie-Victorin & León (1944), Alain (1946b), and Smith (1954). Sprouting vigorously from base after fire. Flowering probably chiefly March through early June, although also November through February.

COMMON NAME. Cereza de sabana (Roig, 1965).

REPRESENTATIVE SPECIMENS. **Cuba.** PINAR DEL RÍO: Sabanalamar, El Sábalo, *Bro. Alain 1329* (GH, US); Sierra de Cabra, on Guane Rd., *Britton et al. 7267* (F, NY, US); between Lagunillas and Luis Lazo, near Río San Sebastian, *Ekman 13813* (S, US); Viñales, Sitio del Infierno, *Ekman 16710* (S, US); San Juan and Martinez, *Ekman 16789* (K, NY, S); S. of Viñales, *Bro. León 14326* (GH, NY, US); Laguna Alcatraz Grande, Remates de Guane, *Bros. León & Marie-Victorin 18720* (GH, US); 11.5 km. S. of Pinar del Río, La Maguina, *Bro. León et al. 17775* (GH, US); Luis Lazo, *O'Donovan 5354* (A, NY, US); near El Guama, *Palmer & Riley 306* (US); Los Palacios to San Pablo de las Yeugas, *Shafer 11928* (MO, NY, US); Arroyo del Sumidero, *Shafer & Bro. León 13679* (F, MO, NY, US). ISLA DE PINOS: Los Indios, *Bros. Alain & Marie-Victorin 31* (GH, US); La Cañada, Sierra de Cañada, *Britton et al. 14410* (F, GH, NY); near Columbia, *Britton et al. 15735* (NY); Las Tunas Mts., *Britton & Wilson 15781* (F, GH, MO, NY, US); San Pedro, *Britton et al. 15806* (F, GH, MO, NY, S, US); Sierra las Casas, E. side of Martí gap, *Cunniff & Bonney* [*Killip no.*] *44817* (US); Santa Barbara, Westport, *Ekman 12097* (NY, S); Nueva Gerona,

at Brazo Fuerte, *Ekman 12245* (F, NY, S, US); between Mina de Oro and Playa del Soldado, *Killip 43906* (US); along Río Las Casas below Nuevo Gerona, *Killip 44020* (US); Siguanea region, *Killip 44046* (US); Júcaro region, *Killip 44546* (IJ, US); Cerro de Mal País, *Bros. León & Marie-Victorin 18863* (GH, US).

Lyonia myrtilloides, a striking and easily recognized plant, is perhaps closest to *L. ekmanii,* from which it is very easily distinguished by its smaller leaves, its more densely pubescent twigs, its narrower capsules, its smaller corollas, and its shorter calyx lobes.

Lyonia myrtilloides is extremely variable in leaf shape and size (also noted by Alain, 1946b). This led Grisebach (1866), when he described the species, to propose that it could be divided into two distinct varieties: var. *parvifolia,* with small, ± narrowly obovate leaves; and var. *ovalifolia,* with larger, widely obovate to widely elliptic or ovate leaves. In addition, he said that var. *ovalifolia* had slightly longer corollas. As more specimens have been collected and plants have been studied in the field, it was realized that there is a complete continuum in leaf size and shape (and in flower size) between the two extremes recognized by Grisebach.

I have chosen the type of *L. myrtilloides* var. *parvifolia* (*C. Wright 2195*) as the lectotype of *L. myrtilloides,* since Grisebach proposed both *L. myrtilloides* var. *parvifolia* and *L. myrtilloides* var. *ovalifolia* at the same time. Several collection dates are given for the lectotype of *Lyonia myrtilloides,* since this "collection" is actually composed of several different collections made by Charles Wright near Viñales at various times between November, 1863, and March, 1864. These collections were lumped for distribution under the number *2195* by Asa Gray; thus the specimens at GOET used by Grisebach in describing the species are from several different collections. It is unfortunately impossible to match the specimens with the proper original collection labels (in C. Wright's handwriting), which are folded in a packet on a sheet at GH, except for the November collection, which is attached to a sheet at NY. The dates enclosed in brackets are not given on the field labels but are those most probable when Wright's itinerary is considered (see Underwood, 1905).

In 1914 Small described *Xolisma* [= *Lyonia*] *vaccinioides* from near Nueva Gerona on the Isle of Pines, separating it from *L. myrtilloides* by the supposedly glaucous lower surface of its leaves. However, the type specimen does not now have glaucous leaves, and there is no notation about this on the label. Jennings (1917) considered *L. vaccinioides* to be limited to the type locality, with all other similar plants of the Isle of Pines and Pinar del Río belonging to *L. myrtilloides.* In contrast, Alain (1946b) treated all the lyonias of the Isle of Pines as *L. vaccinioides,* and the similar plants of Pinar del Río as *L. myrtilloides. Lyonia vaccinioides* is here considered to be a synonym of *L. myrtilloides* because no morphological differences could be seen between the plants of the Isle of Pines and those of Pinar del Río. None of the many specimens collected from the Isle of Pines has glaucous leaves.

29. **Lyonia maestrensis** Acuña & Roig, Contr. Ocas. Mus. Hist. Nat. Col. La Salle **15:** 5. 1956. TYPE: Cuba, prov. Oriente, near Yao Arriba, 13 March 1952, *E. E. Smith 375* (holotype, HAC, not seen).

Evergreen small shrub to tree with longitudinally furrowed bark. Twigs slightly to moderately angled, slender, sparsely lepidote, otherwise glabrous to sparsely pubescent. Buds ovoid, 0.8–1.2 by 0.8 mm., lepidote. Leaf blades ovate to elliptic, 3.5–9 by 2–6 cm., ± flat, usually thinly coriaceous, ca. 0.15–0.2 mm. thick; apex acuminate, acute, to rounded or truncate; base broadly cuneate to slightly cordate; margin not revolute, distal portion clearly but finely and irregularly toothed, proximal portion obscurely toothed; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales quickly deciduous, sparsely pubescent on proximal portion of midvein, with 2° and higher order veins obscure to slightly visible; abaxial surface sparsely lepidote, otherwise glabrous, the 3° and higher order veins ± flat, obscure to very slightly and laxly reticulate, the 2° veins visible and slightly raised to obscure; scales rusty to golden, becoming whitish with age, usually persistent, ca. 0.08–0.17 mm. in diameter, entire to slightly irregular; petiole

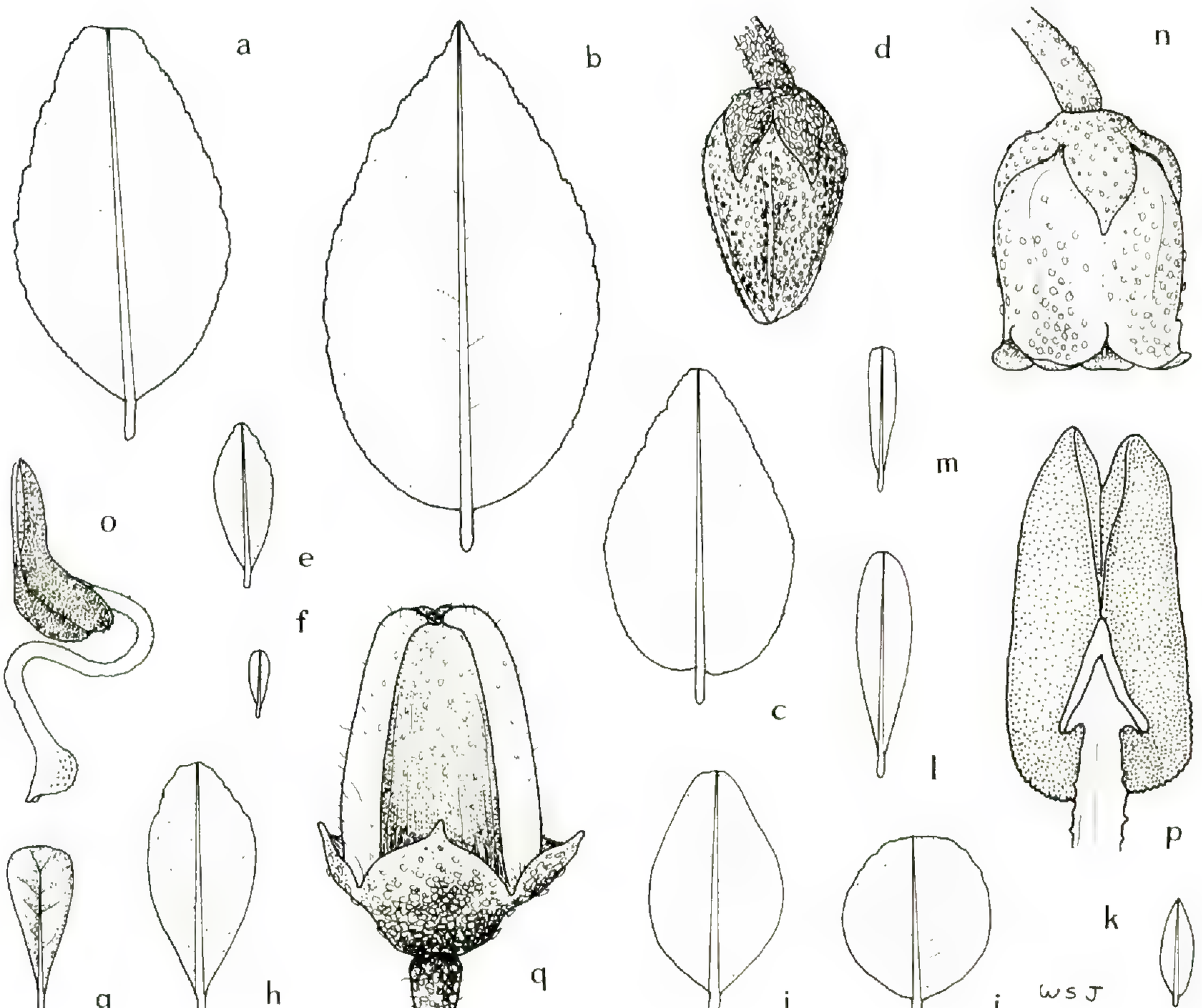


FIGURE 54. a–d, *Lyonia maestrensis:* a–c, leaves, × .5; d, flower bud, × 6. e–q, *L. myrtilloides:* e–m, leaves, × .5; n, flower, × 6; o, stamen, × 12.5; p, anther, × 25; q, capsule, × 6.

2–6 mm. long, lepidote, otherwise adaxially pubescent. Inflorescences fasciculate, ca. 3- to 8(?)-flowered. Pedicels ± clearly articulated with calyx, slender, ca. 2.5–3.5 mm. long, lepidote, otherwise sparsely pubescent; bracteoles opposite, basal, narrowly triangular, ca. 0.8 mm. long; bracts to ca. 1(?) mm. long. Flowers 4-merous; calyx lobes triangular, with acuminate to nearly acute apices, 0.7–0.9 by 0.4–0.6 mm., the adaxial side glabrous or very sparsely pubescent near apex, the abaxial side lepidote, otherwise usually glabrous; corolla urceolate, only immature flowers seen, but possibly reaching 3 or 4 mm. in length, white, abaxially moderately (or densely?) lepidote; filaments roughened; ovary lepidote, otherwise pubescent. Capsule narrowly ovoid, ca. 8 by ca. 3.5 mm., lepidote, otherwise pubescent, with pale, very thick sutures; seeds not seen. (FIGURE 54.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, western Sierra Maestra (MAP 27). Rare; in "fangales" (moist montane forests).

SPECIMENS EXAMINED. **Cuba.** ORIENTE: Sierra Maestra, on divide between Río Yara and Río Plata, *Ekman 14282* (S); Pico Turquino region, *Bro. León 10960* (GH, NY, US).

The relationships of this rare and poorly known species to the other taxa of sect. LYONIA are problematic. It may be related to *Lyonia latifolia* or *L. elliptica*, but at present the plant is too poorly collected to determine the full range of morphological variation of its leaves, flowers, and fruits. The single specimen with mature capsules (the type) has not been available for examination.

30. **Lyonia latifolia** (A. Rich.) Griseb. Catal. Pl. Cubens. 51. 1866.

Evergreen low shrub to moderate-sized tree to ca. 6 meters tall, with brownish to gray, longitudinally furrowed bark. Twigs slightly to moderately angled, slender, densely to moderately lepidote, otherwise slightly to occasionally moderately pubescent. Buds ovoid, 1–2.5 by 1–2.5 mm. Leaf blades ovate to obovate, or nearly orbicular, 2.5–7(–9.5) by 1.5–5(–6.5) cm., ± flat, coriaceous, ca. 0.34–0.43 mm. thick; apex acuminate, acute, to rounded or truncate; base slightly cordate to narrowly cuneate or attenuate; margin plane to slightly revolute, distal portion entire to very obscurely and irregularly toothed, proximal portion entire to undulate; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales quickly deciduous, moderately pubescent on proximal portion of midvein, the 3° and higher order veins obscure to visible, the midvein sometimes slightly depressed, the 2° veins obscure to visible, ± flat to slightly depressed; abaxial surface densely to sparsely lepidote, otherwise densely pubescent (occasionally only sparsely pubescent near margin or apex), the 3° and higher order veins ± flat or nearly so and obscure to slightly and laxly reticulate (or, on few plants from extremely high elevations, raised and forming dense, fine reticulum), the 2° veins slightly raised and visible to occasionally nearly obscure; scales yellowish gold, sometimes becoming whitish with age, deciduous, ca.

0.08–0.43 mm. in diameter, nearly entire to erose; petiole 4–20 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, ca. 1- to 12-flowered. Pedicels clearly articulated with calyx, moderately stout, 2.5–10 mm. long, densely lepidote, otherwise pubescent; bracteoles ± opposite, basal, narrowly triangular, 1.2–3.6 mm. long; bracts to ca. 2.5 mm. long. Flowers (4- or) 5- (or 6-)merous (in occasional plants 4- and 5-merous); calyx lobes narrowly triangular, with acute or long-acuminate apices, (2.5–)3.5–7(–8) by 0.8–2.5 mm., the adaxial side densely lepidote, otherwise sparsely to densely pubescent, especially near apex, the abaxial side very densely lepidote, otherwise pubescent; corolla long-urceolate, 5.5–8 by 3–6 mm., white to pink but appearing yellow or golden due to peltate scales, abaxially densely lepidote; filaments roughened, 3–5 mm. long, unappendaged or with minute spurs near anther-filament junction, anthers 1.3–2 mm. long; ovary lepidote and pubescent, placentae ± subapical. Capsules ovoid to short-ovoid or subglobose, 4–6(–7) by 3.5–5.5(–6) mm., lepidote, otherwise moderately to densely pubescent, the pale, very thick sutures separating as unit from adjacent valves; seeds 1.5–2.7 mm. long.

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente; Sierra Maestra, Gran Piedra range, and few mountains of eastern Oriente. Pinelands, thickets, rocky places, moist montane forests ("fangales"), "monte fresco" vegetation of higher summits; ca. 650–2000 m. alt.

Key to the Varieties of *Lyonia latifolia*

1. Leaves with secondary veins at least slightly depressed, the blade ovate to elliptic or nearly orbicular, with length/width ratio of 1–1.9, and with base rounded, slightly cordate, or broadly cuneate, not decurrent, the petiole 4–12 mm. long; [Sierra Maestra from Loma del Gato westward]. . . . . 30a. var. *latifolia*.

1. Leaves with secondary veins not depressed, the blade elliptic to obovate or ovate, with length/width ratio of (1.2–)1.4–2.4(–2.7), and with base narrowly to broadly cuneate, or less commonly rounded, sometimes decurrent; the petiole 8–20 mm. long; [Sierra Maestra from Loma del Gato east to Gran Piedra range and mts. of eastern Oriente]. . . . . 30b. var. *calycosa*.

30a. **Lyonia latifolia** (A. Rich.) Griseb. var. **latifolia**

Leucothoë latifolia A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11:** 74. 1850 [1851]. *Andromeda latifolia* (A. Rich.) C. Wright in Sauvalle, Anal. Acad. Ci. Habana **6:** 249. 1870. *Xolisma latifolia* (A. Rich.) Small, N. Am. Fl. **29**(1): 70. 1914. TYPE: Cuba, [prov. Oriente], Sierra Maestra, near Mogote, Santiago de Cuba, 700 hexap. alt., April 1844, *Linden 1693* (holotype, P!; fragments of holotype, F!, L!; isotypes, K!, NY!, W!; fragment of isotype, NY!).

Xolisma turquini Small, Jour. New York Bot. Gard. **23:** 92. 1922. *Lyonia*

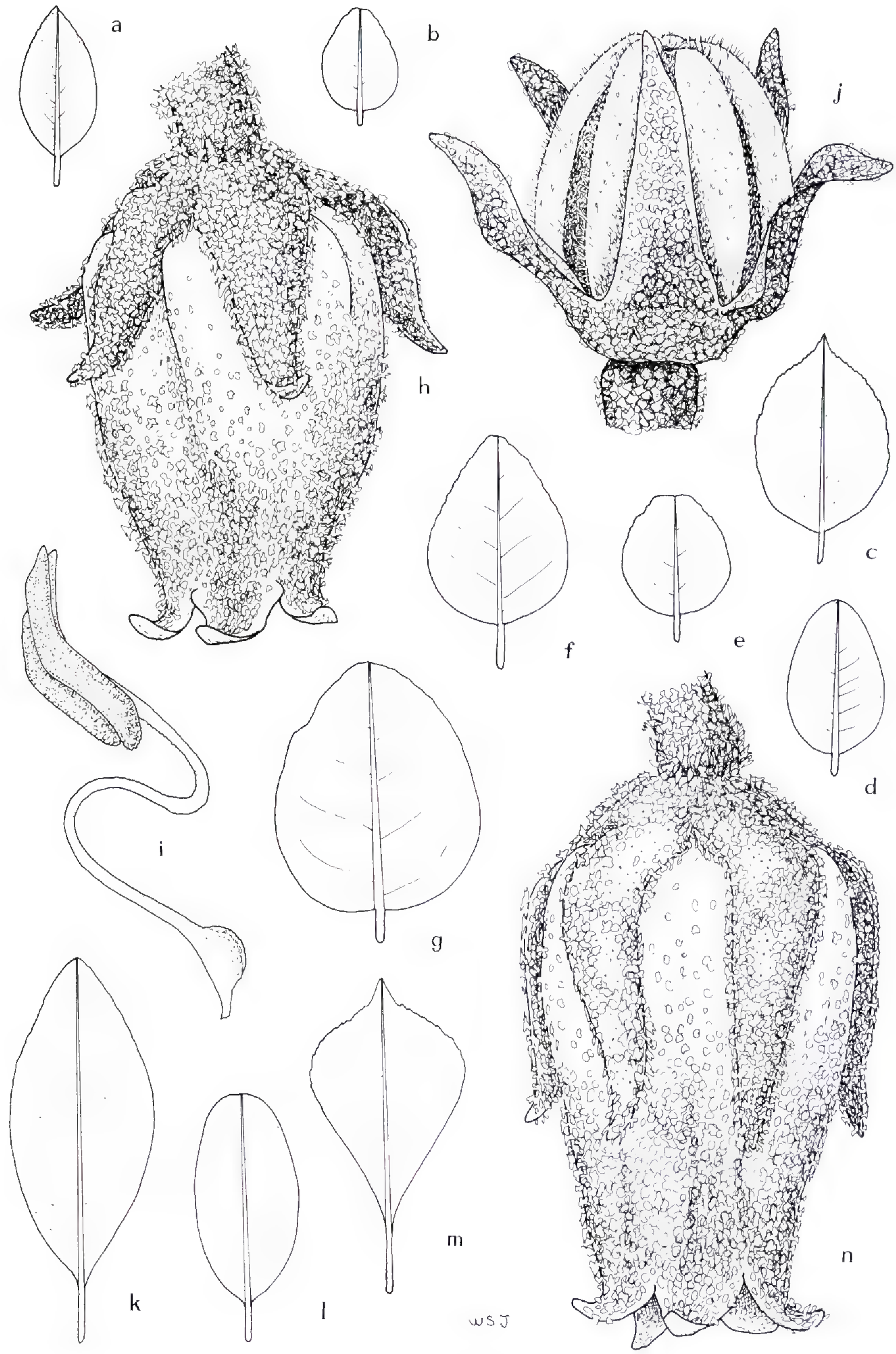


FIGURE 55. a–j, *Lyonia latifolia* var. *latifolia:* a–g, leaves, × .5; h, flower, × 6; i, stamen, × 12.5; j, capsule, × 6. k–n, *L. latifolia* var. *calycosa* (in part): k–m, leaves, × .5; n, flower, × 6.

turquini (Small) Ekman ex Urban, Repert. Sp. Nov. **22:** 42. 1925. TYPE: Cuba, prov. Oriente, first peak of Pico Turquino, ca. 7050 ft. alt., 10 April 1922, *Bucher 9* (holotype, NY!).

Lyonia densiflora Urban, Repert. Sp. Nov. **22:** 42. 1925. TYPE: Cuba, prov. Oriente, Sierra Maestra, in Pinar de Papayo, ca. 800 m. alt., 22 June 1918, *E. L. Ekman 9262* (holotype, S!; isotype, NY!).

Lyonia clementis Acuña & Roig, Contr. Ocas. Mus. Hist. Nat. Col. La Salle **15:** 4. 1956. TYPE: Cuba, prov. Oriente, Sierra Maestra, near Loma del Gato, August 1932, *Bro. Clemente s.n.* (holotype, HAC, not seen).

Leaf blades ovate or widely ovate to elliptic or nearly orbicular, 2.5–6.5(–8) cm. long; base rounded to slightly cordate or broadly cuneate, not decurrent; adaxial surface with midvein usually slightly depressed, 2° veins usually at least slightly depressed (especially on larger-leaved plants); abaxial surface with 3° and higher order veins ± flat or nearly so and obscure to slightly and laxly reticulate (in plants from extremely high elevations near or at summit of Pico Turquino, raised, forming dense, fine reticulum); petiole 4–12(–14) mm. long, pubescent adaxially only. Pedicels 2.5–5(–7) mm. long. Calyx lobes (3–)3.5–7(–8) mm. long. (FIGURE 55; see also Sagra (1850).)

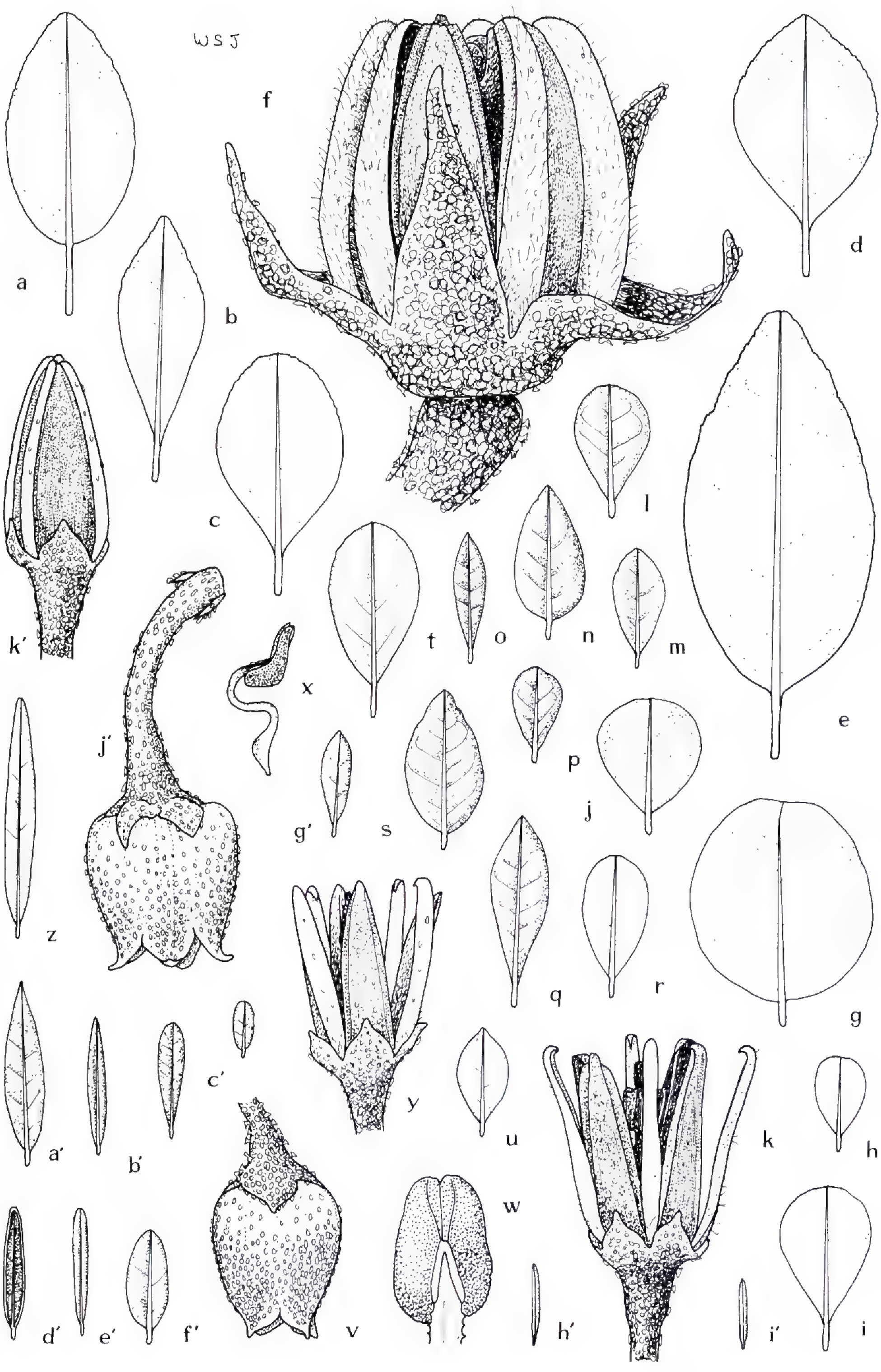
DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra Maestra from Loma del Gato westward (MAP 27). Pinelands (of *Pinus maestrensis*), low to tall thickets, moist montane forests ("fangales"), rocky areas, "monte fresco" vegetation of higher summits; ca. 700–2000 m. alt. "Monte fresco" thickets on summit of Pico Turquino above zone of persistent fog and mist; vegetation less dense, lower, and with more wind circulation than in more humid "fangales" on lower slopes. High-elevation form of this variety locally common in this zone. Other characteristic species listed by Borhidi & del Risco (1979), Bucher (1922), León (1924, 1946), Seifriz (1943), Conde (1952), and Smith (1954). Humid montane forest of Loma del Gato described in León (1922); general characteristics of "fangales" given by Seifriz (1943) and León (1946). Flowering probably mainly April to July.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Sierra Maestra, top of Pico Turquino, *Acuña 6763* (NY); Loma del Gato, *Bucher 254A* (NY); summit, La Bayamesa, *Ekman 7149* (K, NY, S); N. of Pico Turquino, steep cliffs, *Ekman 14588* (S); near Pico Turquino, *Bro. León 10786* (GH).

30b. **Lyonia latifolia** (A. Rich.) Griseb. var. **calycosa** (Small) Judd, comb. et stat. nov.

Xolisma calycosa Small, N. Am. Fl. **29**(1): 67. 1914. *Lyonia calycosa* (Small) Urban, Repert. Sp. Nov. **22:** 42. 1925. TYPE: Cuba, prov. Oriente, between

FIGURE 56. a–f, *Lyonia latifolia* var. *calycosa* (in part): a–e, leaves, × .5; f, capsule, × 6. g–k, *L. toaënsis:* g–j, leaves, × .5; k, capsule, × 6. l–y, *L. glandulosa* var. *glandulosa:* l–u, leaves, × .5; v, flower, × 6; w, anther, × 25; x, stamen, × 12.5; y, capsule, × 6. z–k′, *L. glandulosa* var. *revolutifolia:* z–i′, leaves, × .5; j′, flower, × 6; k′, capsule, × 6.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Firmeza and Gran Piedra, 4, 5 March 1911, *Shafer 8997* (holotype, NY!; isotypes, F!, NY (3 sheets)!, US!).

Lyonia elata Urban, Repert. Sp. Nov. **22:** 41. 1925. TYPE: Cuba, prov. Oriente, Sierra Maestra, Manacal, near Alto de Comejan, ca. 1100 m. alt., 7 July 1918, *E. L. Ekman 9372* (holotype, S!; isotypes, K!, NY!, S!, US!).

Lyonia leonis Acuña & Roig, Contr. Ocas. Mus. Hist. Nat. Col. La Salle **15:** 4. 1956. TYPE: Cuba, prov. Oriente, Sierra Maestra, Loma del Gato, 950–1000 m. alt., July 1921, *Bro. León, Bro. Clemente, & M. Roca 10387* (holotype, HAC, not seen; isotypes, GH!, NY!).

Leaf blades elliptic to ovate or obovate, 3.5–7(–9.5) cm. long; base narrowly to broadly cuneate or less commonly rounded, sometimes decurrent; adaxial surface with midvein not depressed, 2° veins usually not depressed; abaxial surface with 3° and higher order veins ± flat or nearly so and obscure to slightly and laxly reticulate; petiole (7–)8–20 mm. long, pubescent adaxially or all around. Pedicels 4–10 mm. long. Calyx lobes (2.5–)3.5–6(–6.5) mm. long. (FIGURES 55, 56.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra Maestra from Loma del Gato east to Gran Piedra range and Alto de Iberia, Sierra de Cristal, and Sierra de Imias (MAP 27). Moist montane forests ("fangales"), thickets, and pinelands; ca. 650–1250 m. alt. Flowering chiefly March and April.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: near Olimpo, Gran Piedra Mts., *Bro. Clemente 7238* (GH, US); Sierra de Cristal, near Río Lebisa, *Ekman 6858* (NY); Alto de Iberia, *Ekman 8313* (S); Sierra Maestra, near Gran Piedra, *Ekman 8799* (NY, S); Sierra de Imías, Anubón del Mate, *Bro. León 12191* (NY).

Lyonia latifolia is rather distinctive because of the beautiful yellowish gold peltate scales that densely cover the young leaves, the long-urceolate corollas, and both surfaces of the very elongated calyx lobes. It is probably related to *L. obtusa, L. nipensis, L. macrophylla*, and the elevationally isolated *L. affinis* (FIGURE 3). *Lyonia affinis* has calyx lobes that are shorter and that are not adaxially lepidote, corollas that are more or less cylindrical and more sparsely lepidote, and leaves that are differently shaped; there are also some anatomic distinctions (TABLE 8).

Lyonia latifolia var. *calycosa* can be differentiated from var. *latifolia* by its leaves, which are often longer in relation to their width, and with secondary veins not depressed, and by its usually longer petioles and pedicels. Since these taxa are distinguished by slight (but fairly consistent) vegetative differences, and since their flowers and fruits are essentially identical and quite different from those of any other species, they are best considered to be varieties of a variable species. Although the varieties are geographically isolated (MAP 27), they both occur on Loma del Gato, where collected specimens of the two are quite similar, possibly from interbreeding; in some respects the division between the two taxa is rather arbitrary at this locality. *Clemente 5516* (NY) and *Ekman 7005* (S), both from the Loma del Gato, probably represent intermediate plants. *León, Clemente, & Roca 10387* (the type of *L. leonis*

Acuña & Roig) resembles var. *calycosa* in most respects but has a few leaves with slightly depressed secondary veins. From the original description, *L. clementis* Acuña & Roig appears to be closest to *L. latifolia* var. *latifolia*, but pedicel length is given as 6–7 mm., longer than usual for this taxon, and petiole length, given as 10–14 mm., is longer than that of any other specimen of this variety seen by the author. *Lyonia clementis* is thus tentatively treated as a synonym of *L. latifolia* var. *latifolia*, but final placement awaits field study of populations of *L. latifolia* and investigation of the type specimen at HAC. In other areas, where these two taxa are geographically separated, there is no difficulty in distinguishing them.

Plants of *Lyonia latifolia* var. *latifolia* from 1800–2000 meters altitude often have smaller leaves having the secondary veins only very slightly depressed and the abaxial surface with a fine network of raised veins. Such plants have been called *L. turquini* by Small (1922) and Roig & Acuña (1957), but there is no morphological break between these plants and those of lower elevations. Although most plants of this variety are densely pubescent on the abaxial leaf surface, occasional individuals (e.g., *Ekman 5279* and *Ekman 9262*) are only very sparsely pubescent.

Lyonia latifolia var. *calycosa* is quite variable in leaf shape, especially in apex and base type. Plants with rounded, acute, or strongly acuminate leaf apices, and rounded to narrowly cuneate or attenuate bases have all been collected from the geographically limited Gran Piedra range. As with var. *latifolia*, there is a tendency for some plants to have only a very sparse covering of unicellular hairs on the abaxial leaf surface. This is seen even in the type collection of *Xolisma calycosa* Small (*Shafer 8997*), all the branches of which have leaves densely pubescent beneath (the isotype at F, however, is nearly glabrous).

31. **Lyonia toaënsis** Acuña & Roig, Contr. Ocas. Mus. Hist. Nat. Col. La Salle **15:** 5. 1956. TYPE: Cuba, prov. Oriente, at Laguna Galano, La Alegría, Toa, 2 January 1954, *Bro. Alain 3853* (holotype, HAC, not seen; isotypes, GH!, NY!).

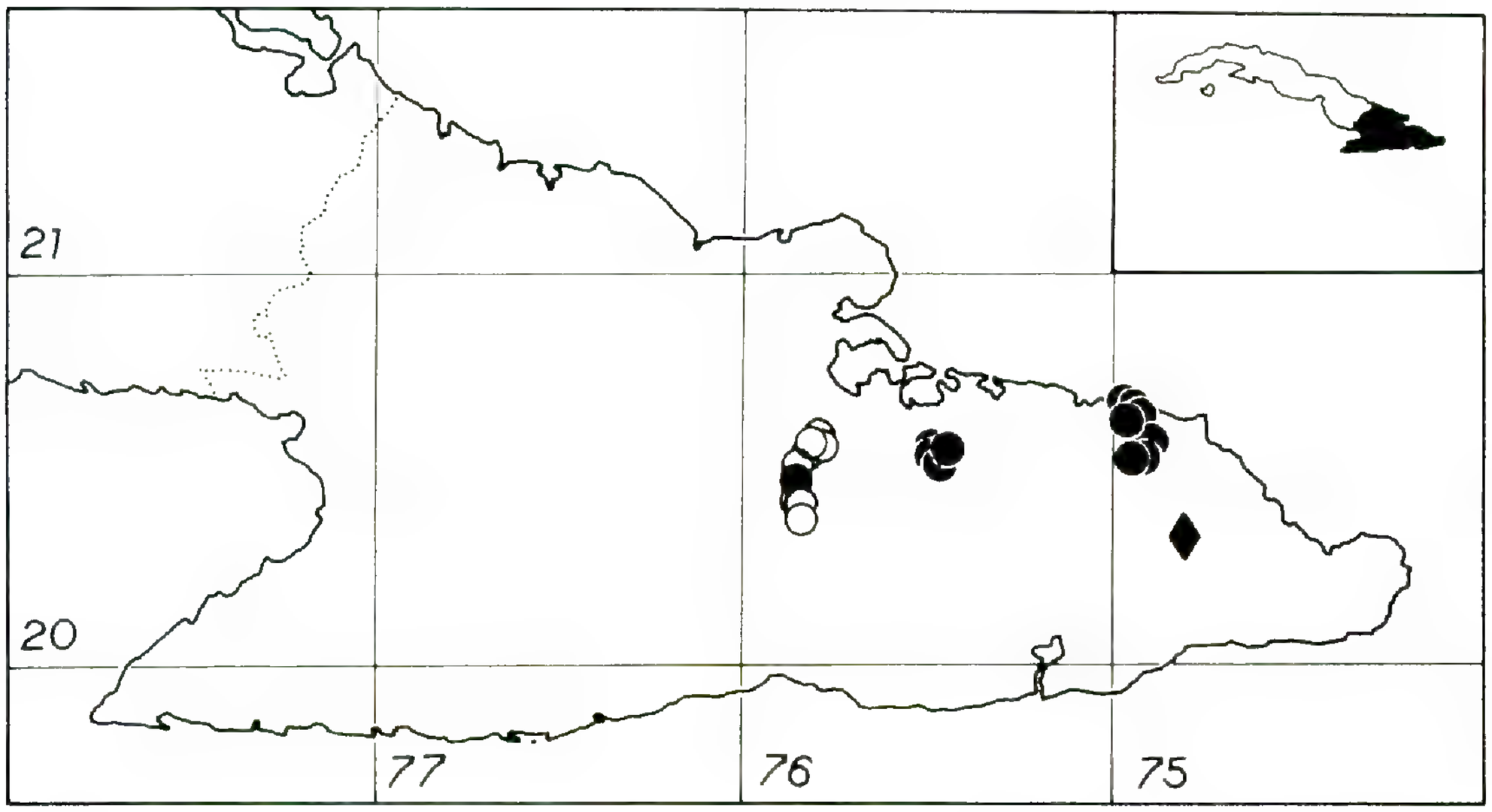
Evergreen small tree or shrub, with longitudinally furrowed bark. Twigs slightly to moderately angled, slender, sparsely to moderately lepidote, otherwise moderately to densely pubescent. Buds ovoid, 0.7–1.1 by ca. 0.6 mm. Leaf blades obovate to widely obovate or orbicular, 2–5 by 1–4.8 cm., ± flat, coriaceous, ca. 0.36–0.48 mm. thick; apex rounded to truncate; base cuneate to rounded; margin usually plane, entire; venation brochidodromous, 3° veins reticulate; adaxial surface lepidote but scales quickly deciduous, with moderate to dense pubescence on midvein, especially proximal portion, often extending to some 2° and 3° veins, the 3° and higher order veins obscure to visible, the midvein usually not depressed, the 2° veins obscure to slightly visible, not depressed; abaxial surface moderately lepidote, otherwise densely pubescent, the 3° and higher order veins ± flat, obscure to less commonly very slightly and laxly reticulate, the 2° veins obscure to slightly raised and visible; scales rust colored, often becoming whitish with age, persistent, ca.

0.1–0.17 mm. in diameter, irregular; petiole 4–6 mm. long, lepidote, otherwise pubescent all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, 1- to 6-flowered. Pedicels lacking visible articulation with calyx and appearing swollen just below capsule, slender, 2–5.5 mm. long, lepidote, otherwise sparsely pubescent; bracteoles subopposite, nearly basal, narrowly triangular, to ca. 0.7 mm. long; bracts to ca. 0.8 mm. long. Flowers 4-merous; calyx lobes triangular, with acuminate apices, 0.7–0.9 by 0.4–0.6 mm., the adaxial side glabrous or very sparsely pubescent near apex, the abaxial side moderately lepidote, otherwise glabrous; corolla not seen but probably to ca. 3 mm. long, urceolate, white, abaxially sparsely lepidote; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule narrowly ovoid, 2.5–4 by 1–2 mm., lepidote, otherwise sparsely pubescent, especially near base, the very thick sutures separating as unit from adjacent valves; seeds to 2 mm. long. (FIGURE 56.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Pico Galano in Sierra del Frijol (near La Alegría) (MAP 29). High, dense thickets or moist montane forests, often enveloped in fog; ca. 1000–1200 m. alt. Brief account of vegetation of Pico Galano given in Alain (1954).

ADDITIONAL SPECIMENS EXAMINED. **Cuba.** ORIENTE: summit of Pico Galano, Sierra del Frijol, La Alegría, Toa, *Bro. Alain 3756* (GH, NY).

Lyonia toaënsis is closely related to *L. glandulosa*, from which it can be readily distinguished by its orbicular to broadly obovate, blunt-tipped, flat leaves with plane margins and secondary veins not depressed. In addition, its leaves are usually less than twice as long as wide and lack persistent thickened bases of peltate scales on the adaxial surface. The taxa are



MAP 29. Distribution of *Lyonia glandulosa* var. *glandulosa* (circles), *L. glandulosa* var. *revolutifolia* (dots), and *L. toaënsis* (diamond).

geographically isolated, since *L. toaënsis* has only been collected from at or near the summit of Pico Galano, in the Sierra del Frijol, while *L. glandulosa* occurs in the sierras de Nipe, Mícara, Cristal, and Moa, and in the vicinity of Moa. Both taxa are characterized by the lack of an articulation between the pedicel and calyx and by very small, narrowly ovoid capsules.

32. **Lyonia glandulosa** (A. Rich.) Urban, Repert. Sp. Nov. **22:** 46, 47. 1925.

Evergreen shrub to ca. 3.5 meters tall, with longitudinally furrowed bark. Twigs slightly to moderately angled, slender, densely lepidote, otherwise glabrous to densely pubescent. Buds ovoid, 0.6–1 by 0.5–0.8 mm. Leaf blades obovate to elliptic or narrowly elliptic, 1–4(–5.5) by 0.3–2(–3) cm., usually slightly to strongly recurved, coriaceous, ca. 0.3–0.44 mm. thick; apex acute to rounded or truncate; base narrowly to broadly cuneate to rounded; margin plane to strongly revolute, entire to undulate; venation brochidodromous, 3° veins ± reticulate; adaxial surface roughened by raised-reticulate pattern of 3° veins and/or thickened persistent scale bases (sometimes only clearly developed near margin or apex of leaf), lepidote but scales quickly deciduous, sparsely to moderately pubescent on proximal portion of midvein, the 3° and higher order veins forming ± raised reticulum or less commonly nearly obscure, the midvein usually depressed, the 2° veins visible to occasionally obscure, usually at least few per leaf slightly to strongly depressed; abaxial surface moderately lepidote, otherwise densely pubescent, the 3° and higher order veins ± flat, usually obscure, the 2° veins slightly raised and visible or less commonly obscure; scales rust colored, often becoming whitish with age, persistent, ca. 0.1–0.22 mm. in diameter, ± irregular; petiole 1.5–5.5 mm. long, lepidote, otherwise pubescent adaxially or all around. Flower buds above or intermixed with vegetative buds; inflorescences fasciculate, 1- to 7-flowered. Pedicels lacking visible articulation with calyx and appearing swollen just below capsule, slender, 1.5–7 mm. long, lepidote, otherwise glabrous to moderately pubescent; bracteoles subopposite, nearly basal, narrowly triangular, 0.5–0.8 mm. long; bracts to ca. 0.8 mm. long. Flowers 4- (or 5-)merous; calyx lobes triangular, with acuminate apices, 0.5–1 by 0.4–0.6 mm., the adaxial side glabrous to very sparsely pubescent, especially toward margins or apex, the abaxial side densely lepidote; corolla urceolate to cylindrical, 2–3 by 1–2.2 mm., white, abaxially sparsely lepidote; filaments roughened, 1–1.5 mm. long, unappendaged or with very minute spurs near anther-filament junction, anthers 0.7–0.9 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule narrowly ovoid, 2.5–4.5 by 1–2 mm., lepidote, otherwise very sparsely pubescent (sometimes limited to few hairs near base), the pale, very thick sutures separating as unit from adjacent valves; seeds 1.5–2.4 mm. long.

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente; Sierra de Nipe, Sierra de Cristal, Sierra de Mícara, Sierra de Moa, and limonite plateau near Moa. Thickets, stream sides, grassy areas, *Pinus cubensis* savannas; ca. 300–1100 m. alt.

Key to the Varieties of *Lyonia glandulosa*

1. Leaves obovate to less commonly elliptic, 0.5–2 cm. wide, from 1.5–3(–3.5) times as long as wide, distal margin usually plane or only slightly revolute; [Sierra de Nipe] . . . . . 32a. var. *glandulosa.*
1. Leaves elliptic to narrowly so, usually not over ca. 1 cm. wide, from 2.5–7(–10) times as long as wide, distal margin slightly to strongly revolute; [chiefly in Sierra de Mícara, Sierra de Cristal, Sierra de Moa, and vicinity of Moa] . . . . . 32b. var. *revolutifolia.*

32a. **Lyonia glandulosa** (A. Rich.) Urban var. **glandulosa**

Leucothoë glandulosa A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11:** 74. 1850 [1851]. *Andromeda glandulosa* (A. Rich.) C. Wright in Sauvalle, Anal. Acad. Ci. Habana **6:** 249. 1870. TYPE: Cuba, prov. Oriente, Pinal, near Santiago de Cuba, May 1844, *Linden 1778* (holotype, P!; isotypes, L (from fragment at P)!, P (2 sheets)!, W!).

Twigs glabrous to moderately pubescent. Leaf blades obovate to elliptic, 1.5–3.5(–4.5) by 0.5–2(–3) cm., usually slightly to moderately recurved, length/width ratio 1.5–3(–3.5); base narrowly to broadly cuneate; margin not revolute distally to clearly so, slightly to strongly revolute proximally. Pedicels glabrous to sparsely pubescent. (FIGURE 56.)

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, Sierra de Nipe (MAP 29). Thickets, stream sides, grassy areas, *Pinus cubensis* savannas; ca. 450–800 m. Vegetation of this mountain range described by Carabia (1945). Flowering chiefly March to July.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: Sierra de Nipe, near Río Piloto, *Ekman 2044* (NY, S); between Río Piloto and Brazo Dolores, *Ekman 5714* (K, S); Loma Mensura, *Ekman 9064* (NY, S); Cayo La Plancha, *Bros. León & Alain 19980* (GH, US); crest of Sierra de Nipe, *Morton & Acuña 3104* (UC); near Woodfred, *Shafer 3014* (GH, MO, NY, S); Arroyo del Medio, above falls, *Shafer 3636* (NY); Pinal de Mayarí, *Wright 1635,* in part (F, GH, GOET, NY, S, UC).

32b. **Lyonia glandulosa** (A. Rich.) Urban var. **revolutifolia** Judd, var. nov.

Varietas haec ab Lyonia glandulosa (A. Rich.) Urban var. glandulosa differt foliis ellipticis vel anguste ellipticis minus quam ca. 1 cm. latis, ca. 2.5–7(–10) plo longioribus quam latioribus, marginibus distalibus foliorum parum vel valde revolutis.

Twigs slightly to densely pubescent. Leaf blades elliptic to narrowly so, to rarely narrowly obovate, 1–4(–5.5) by 0.3–1(–1.7) cm., usually slightly to strongly recurved; base narrowly to broadly cuneate to rounded; margin slightly to strongly revolute. Pedicels sparsely to moderately pubescent. (FIGURE 56.)

TYPE: Cuba, prov. Oriente, Sierra de Moa, pine-barrens, 900 m. alt., 24–27 July 1953, *Bro. Alain 3418* (holotype, GH!; isotype, US!).

DISTRIBUTION AND ECOLOGY. Cuba, prov. Oriente, chiefly in sierras de Mícara, Cristal, and Moa, and limonite plateau near Moa, but also few collections from Sierra de Nipe (MAP 29). Thickets, stream sides, open pinelands of *Pinus cubensis,* on reddish lateritic soils developed through weathering of underlying serpentine rocks; ca. 300–1100 m. Vegetation of Moa plateau described in León (1941, 1946), Marie-Victorin (1942, 1944), Alain (1946a), Webster & Jervis (1952), and Marie-Victorin & León (1956). Flowering probably March or April to late June or early July.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: near Moa, Camino Cayo Coco, *Acuña 12654* (US); near Moa, Camino Gran Tierra, *Acuña 12655* (US); Sierra de Moa, pine-barrens, *Bro. Alain 3409* (GH, US); Río Yagrumajes, Moa, *Bros. Clemente & Alain 3863* (GH, US); Mina Franklin, Moa, *Bros. Clemente & Alain 3896* (GH); Sierra de Nipe, near Río Piedra, *Ekman 1822* (S); Sierra del Cristal, at tributary of Río Lebisa, *Ekman 15970* (S); Sierra de Mícara, *Ekman 16018* (K, NY, S, US); Sierra de Cristal, between Los Mulos and La Corea, camino de Mayarí, *López-Figueiras 252* (US); El Gurugú, Sierra de Nipe, *López-Figueiras 2581* (US); La Breña, Moa, *Bro. León et al. 22543* (GH, US); Moa, plateau between Río Cabanas and Río Moa, *Bros. Marie-Victorin & Clemente 21754* (US).

Lyonia glandulosa is clearly related to the geographically isolated *L. toaënsis,* from which it differs in its more revolute leaves that are usually slightly to strongly recurved, with more depressed secondary veins and acute to rounded apices.

Lyonia glandulosa var. *revolutifolia* can easily be distinguished from var. *glandulosa* by its more narrowly elliptic and revolute leaves (see FIGURES 56 and 57). In addition, the roughening of the adaxial leaf surface by the thickened bases of peltate scales is more strongly developed in var. *glandulosa.* The two taxa are essentially allopatric, with var. *glandulosa* endemic to the Sierra de Nipe and var. *revolutifolia* occurring chiefly in the Moa plateau region and in the sierras de Moa, Mícara, and Cristal.

Since vars. *glandulosa* and *revolutifolia* differ slightly (but consistently) in leaf morphology (as given above), they are considered here as varieties of a single rather variable species. However, there is only a slight discontinuity in the variation pattern of the two taxa (see FIGURE 57), and two collections from the Sierra de Nipe (*Ekman 1822* and *López-Figueiras 2581*) are referable to var. *revolutifolia; Ekman 9530* is somewhat intermediate. Thus, it is possible that further collecting will reveal a more extensive intergradation between the taxa in the few localities where they are possibly sympatric.

Earlier botanists have usually considered var. *revolutifolia* of the Mícara-Moa region to be *Lyonia glandulosa,* and var. *glandulosa* of the Sierra de Nipe to be *L. myrsinifolia.* However, the type of *Leucothoë glandulosa* A. Rich. (1850) actually represents the Sierra de Nipe taxon, while the type of *Leucothoë myrsinifolia* A. Rich. (1850) is here reduced to synonymy under *Lyonia affinis,*

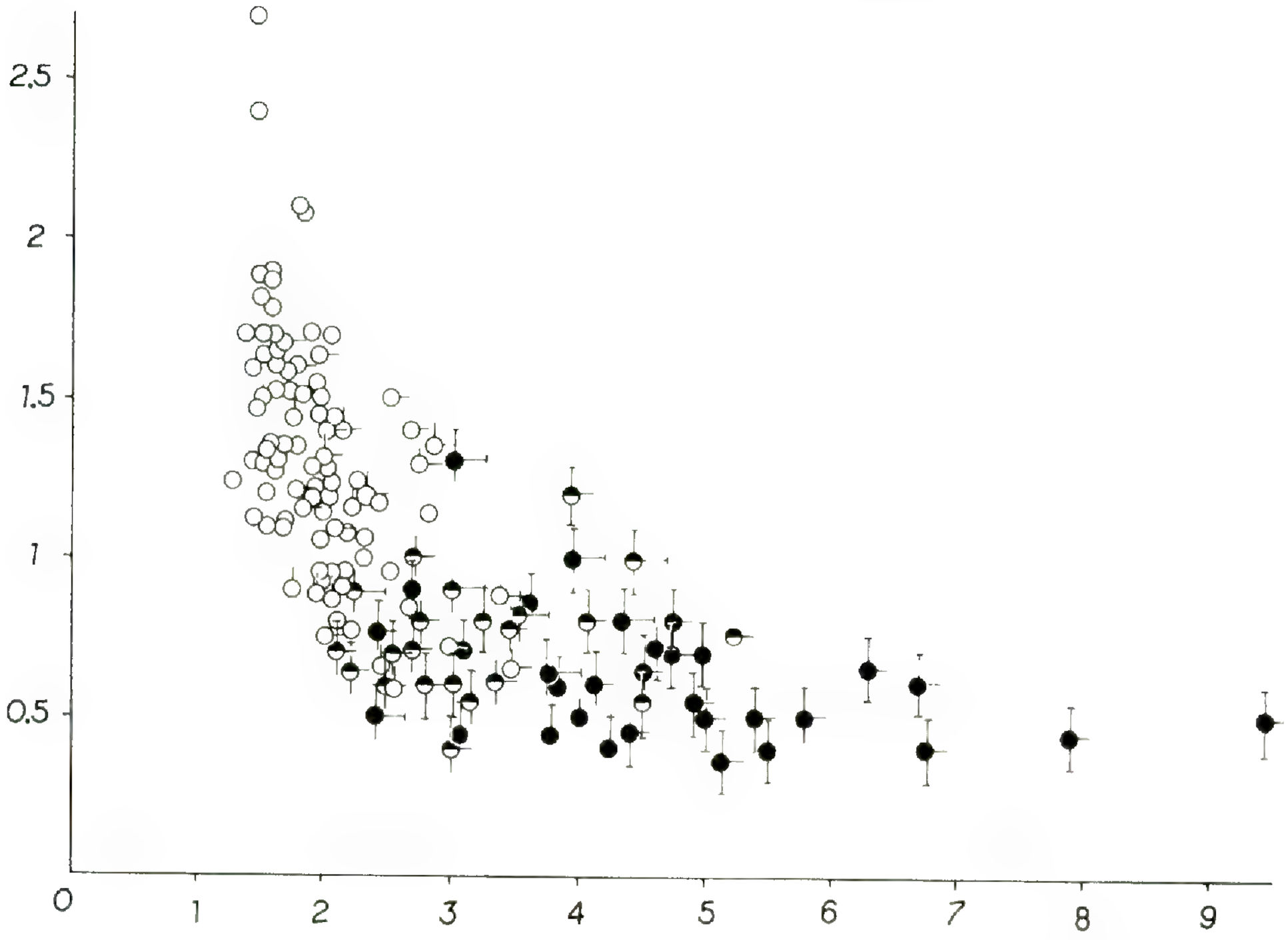


FIGURE 57. Scatter diagram showing variation between *Lyonia glandulosa* var. *glandulosa* and var. *revolutifolia* in six characters. Vertical axis = leaf width in cm.; horizontal axis = length/width ratio of leaf; closed circle = leaf ± narrowly elliptic, half-closed circle = leaf elliptic, open circle = leaf widely obovate to narrowly obovate; full tail to right = adaxial leaf surface ± smooth, no tail to right = thickened bases of peltate scales present on adaxial leaf surface, half tail to right = intermediate; full tail up = distal leaf margin strongly revolute, no tail up = distal leaf margin very slightly revolute or not revolute, half tail up = intermediate; full tail down = Sierra de Moa populations, half tail down = Sierra de Mícara and Sierra de Cristal, no tail down = Sierra de Nipe.

a very distantly related species of the Sierra Maestra. Thus, the name *L. glandulosa* must be used for the plants of the Sierra de Nipe. The plants of the Mícara-Moa region are then left without an epithet; they are here named *L. glandulosa* var. *revolutifolia*.

Sterile specimens of *Lyonia glandulosa* var. *revolutifolia* can sometimes be confused with *L. nipensis* var. *depressinerva*. Such specimens can, upon close inspection, be fairly easily identified, since *L. nipensis* var. *depressinerva* lacks thickened bases of peltate scales on its adaxial leaf surfaces and has two types of peltate scales on its lower leaf surfaces (large, deciduous, erose scales and smaller, persistent, entire ones), while *L. glandulosa* has all scales more or less irregular and persistent. In addition, the two taxa differ slightly in leaf shape and size and in various anatomic characters (e.g., venation, epidermal structure, depression of peltate scales into abaxial leaf surface).

The populations of var. *revolutifolia* from the Sierra de Moa and the limonite plateau near Moa often have slightly longer leaves than do plants of the Sierra de Mícara and Sierra de Cristal.

Although Grisebach (1866) first proposed the combination *Lyonia glandulosa,* this publication was invalid since Grisebach did not accept the name himself but merely listed it as a doubtful species.

33. **Lyonia squamulosa** Martens & Gal. Bull. Acad. Bruxelles **9:** 542. 1842.

Xolisma squamulosa (Martens & Gal.) Small, N. Am. Fl. **29**(1): 66. 1914. TYPE: Mexico, on the lavas, NE. of Cofre de Perote, Veracruz, with pines, at 4000 ft., May, *Galeotti 1797* (holotype, BR?, not seen; isotype, K!, P!, W!; fragment of isotype, L!).

Evergreen shrub to 3(–5) meters tall, usually from underground woody burl or swelling, spreading vegetatively by horizontal underground rhizomes, with longitudinally furrowed bark. Twigs slightly to moderately angled, slender, ± sparsely lepidote, otherwise very sparsely to densely pubescent. Buds ovoid, 1–2 mm. Leaf blades elliptic to ovate or obovate, 1–6.7 by 0.5–3.5 cm., sometimes quite strongly reduced in size toward branch tips, ± flat to very slightly recurved or concave, coriaceous, ca. 0.17–0.26 mm. thick; apex acuminate, acute to rounded; base attenuate, narrowly to broadly cuneate or occasionally rounded; margin usually plane or very slightly revolute, distal portion entire or rarely very obscurely and irregularly toothed, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales quickly deciduous; slightly to densely pubescent on midvein, especially proximal portion, the 3° and higher order veins slightly visible to obscure, the midvein usually not depressed, the 2° veins visible to obscure, usually not depressed; abaxial surface moderately to densely lepidote, otherwise usually glabrous, occasionally with few hairs on midvein, rarely very sparsely to densely pubescent throughout, the 3° and higher order veins flat or nearly so, very slightly and laxly reticulate to obscure, the 2° veins visible to obscure; scales rust colored to dark orange or brownish, sometimes becoming whitish with age, ± persistent, ca. 0.08–0.25 mm. in diameter, erose to entire; petiole 2–9 mm. long, lepidote, otherwise pubescent adaxially to occasionally all around. Floral buds above or intermixed with vegetative buds on previous or present year's growth; inflorescences fasciculate, 2- to 10-flowered. Pedicels clearly articulated with calyx, slender, 4–14 mm. long, lepidote, otherwise glabrous to sparsely pubescent; bracteoles subopposite, basal or nearly so, narrowly triangular, 0.7–1.5 mm. long; bracts to ca. 2 mm. long. Flowers (4- or) 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 1–2 by 0.5–1.8 mm., the adaxial side sparsely to moderately pubescent, especially near apex or margins, the abaxial side lepidote, otherwise glabrous or very sparsely pubescent near base; corolla urceolate, 2.5–5 by 2.5–4.5 mm., white, abaxially sparsely lepidote; filaments roughened, 1.2–2.5 mm. long, unappendaged or with pair of minute spurs near anther-filament junction, anthers 0.7–1.3 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical.

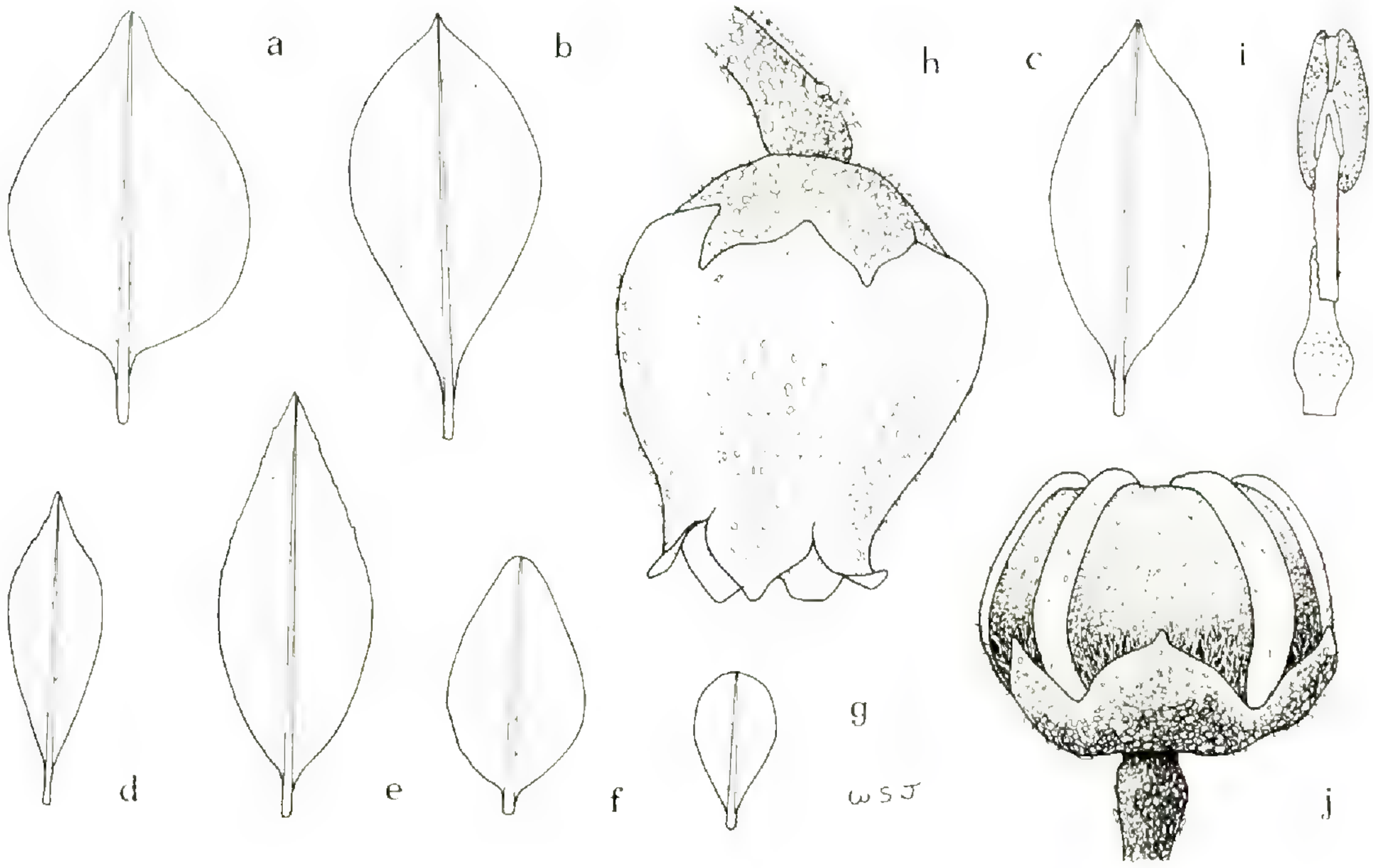
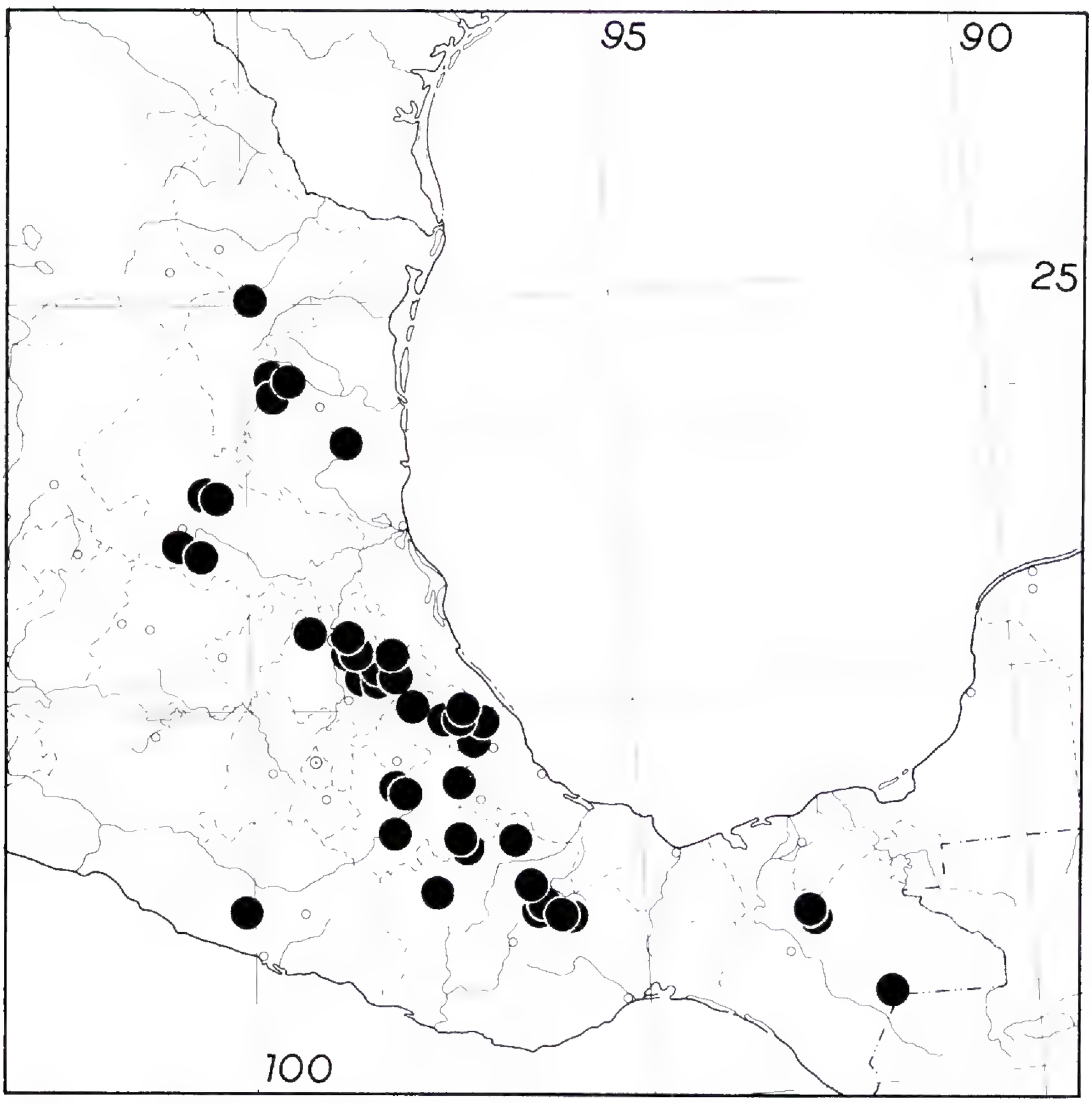


FIGURE 58. *Lyonia squamulosa:* a–g, leaves, × .5; h, flower, × 6; i, stamen, × 12.5; j, capsule, × 6.

Capsule usually subglobose to short-ovoid, 2.5–4(–5) by 2.5–4.5 mm., sparsely lepidote, otherwise usually sparsely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves, sometimes with additional pale lines (one running length of each valve) alternating with and resembling sutures; seeds 1–2 mm. long. (FIGURE 58.)

DISTRIBUTION AND ECOLOGY. Mexico, eastern Sierra Madre from Nuevo León southeast to Veracruz, Puebla, and Oaxaca, Chiapas, and Guerrero (MAP 30). Temperate montane regions, mostly 1000–2400 m. alt. Listed by Miranda and Sharp (1950) as understory shrub of mixed oak and/or pine forests; important in some disturbed communities following destruction of original forest by timber cutting, agriculture, or fire. In studies of vegetation of San Luis Potosí, G. C. Rzedowski (1960) and J. Rzedowski (1966) listed this species as characteristic component of "encinar arbustivo" (chaparral of *Quercus, Arctostaphylos, Cercocarpus, Amelanchier, Garrya, Salvia, Rhus, Yucca*), "piñonar" (forest of *Pinus cembroides*), and "encinar y pinar" (*Pinus* and *Quercus* forests). Also collected from floristically diverse *Pinus-Quercus-Liquidambar* forest of Montebello, Chiapas, described by Carlson (1954); occasionally collected in "bosque deciduo templado" of Sierra Madre Oriental. This forest type described in Miranda and Sharp (1950), J. Rzedowski (1966), and Sarukhán and Pennington (1968). Although not yet reported from Guatemala (Standley & Williams, 1966), may grow there—collected in Montebello area of Chiapas near border. Flowering throughout year but especially March through June.

REPRESENTATIVE SPECIMENS. **Mexico.** NUEVO LEÓN: Cerro del Viejo, 15 mi. W. of Dulces Nombres, municipio Zaragoza, *Meyers & Rogers 3095* (MO); Potrero Redondo, W. to Puerto a Laguna Sanchez, municipio Villa Santiago, *Mueller 2117* (F, GH, MO, TEX, UC); La Trinidad, Montemorelos, *Mueller 3822* (UC). TAMAULIPAS: Los Cerritos to Sierra la Borrada, *Dressler 2007a* (GH); highest part of Sierra de Tamaulipas, rd. from Rancho Las Yucas to Santa Maria de los Nogales, *Martinez & Luyando F-1917* (TEX). SAN LUIS POTOSÍ: Sierra de San Miguelito, near Cueva del Mezquite, *Rzedowski 5451* (ENCB); Cerro Grande, ca. 6 km. NW. of Guadalcázar, *Rzedowski 5956* (ENCB); Mesita de Gallos, ca. 20 km. SE. of Zaragoza, *Rzedowski 6100* (ENCB). HIDALGO: Jacala, *Kenoyer s.n.*, 16 Nov. 1937 (F, MO); El Estribo, Carretera Tulancingo–Tenango, 44 km., *Leyva 536* (ENCB, TEX); vic. of Molango, *Moore 2430* (GH); Tenango de Dória, *Puig 2100* (ENCB); 6 km. SE. of Zacualtipán, *Rzedowski & Madrigal 29457* (ENCB); Cerro de las Cruces, Agua Blanca, *Vela 586* (ENCB). PUEBLA: Serras Decoration Archeveché, near Puebla, *Arsène 1941* (MO, P, US); near



MAP 30. Distribution of *Lyonia squamulosa*.

TABLE 11. **Summary of major morphological, phenological, and geographic differences between Lyonia ferruginea, L. fruticosa, and L. squamulosa.**

CHARACTER	TAXON		
	Lyonia ferruginea	*Lyonia fruticosa*	*Lyonia squamulosa*
Habit	Shrub or small tree to ca. 6(–10) m. tall; branches not rigidly ascending	Small shrub to ca. 1.5(–3) m. tall; branchlets rigidly ascending	Small to moderate-sized shrub to 3(–5) m. tall; branches ± lax to rigidly ascending.
Leaves			
Unicellular indumentum (abaxial surface)	Densely pubescent (occasionally only sparsely so)	Densely pubescent (occasionally only sparsely so; rarely glabrous)	Glabrous (rarely sparsely to densely pubescent)
Size	Not at all or only slightly reduced toward ends of branchlets	Conspicuously reduced toward ends of branchlets	Not to quite strongly reduced toward ends of branchlets
Margin	Slightly to strongly revolute	Plane to less commonly slightly revolute	Plane to less commonly slightly revolute
Curvature of lamina	± Flat to strongly recurved	± Flat to slightly concave (occasionally slightly recurved)	Flat to slightly recurved or concave
Venation			
Adaxial surface	1° and 2° veins usually at least slightly depressed	1° and 2° veins not depressed	1° and 2° veins usually not depressed

Abaxial surface	3° veins often visible but not raised-reticulate	3° veins often nearly as strongly raised as 2°, clearly raised-reticulate	3° veins often visible, sometimes slightly raised-reticulate
Scale type (abaxial surface)	Often of 2 sizes (large, ± irregular, and smaller, nearly entire); at least smaller ones ± persistent, or all ± large and persistent	Not of 2 clearly differentiated size classes; ± moderate sized to large, irregular to nearly entire, deciduous	Not of 2 size classes; ± moderate sized to large, erose to entire, ± persistent
Flowers			
Location	Restricted to previous year's branches (or branches of previous growth-flush)	Usually on present year's branches (or branches of present growth-flush)	On branches of present or previous year's growth(?)
Corolla length (mm.)	2–4 (avg. ca. 2.9)	2.5–5 (avg. ca. 3.3)	2.5–5 (avg. ca. 3.5)
Capsules			
Shape	Ovoid to ellipsoid	± Ovoid to ellipsoid	Usually subglobose to short-ovoid
Length (mm.)	3–6	3–5	2.5–4(–5)
Peak flowering	March and April	May and June (through July)	Ca. March through June
Distribution and ecology	United States, Coastal Plain from South Carolina to Florida; prefers well-drained soils	United States, Coastal Plain from South Carolina to Florida; prefers poorly drained soils	Mexico, chiefly in Sierra Madre Oriental and mts. of Chiapas

Honey Station, *Pringle 13096* (F, GH, L, US); municipio of Pahuatlan, *Puig 5003* (ENCB); Zacapoaxtla, *Salazar s.n.,* 15 April 1913 (US); below Necaxa, *Sharp 45350* (GH); above Coxcatlán, between Apala and top of Cerro Chichiltepec, *Smith et al. 3868* (F, NY). VERACRUZ: Pico Orizaba, *Botteri 975* (P); ridge above Pedregal Esquilon, near Jilotepec, ca. 10 km. N. of Xalapa, *Campbell 3325* (A); near Huayacocotla, *Hernandez & Cedillo 1029* (GH); Santa Ana, Xalacingo, *Vela & Martinez 1189* (ENCB); Paso Enriquez, municipio Yecuaulta, *Ventura 2787* (ENCB, WIS); La Florida, municipio de Atzalán, *Ventura 5655* (DUKE, ENCB, NY). GUERRERO: 10 km. SW. of Amojileca, municipio Chilpancingo, *Rzedowski 23567* (ENCB, MSC). OAXACA: Cumbre de Huehuetlán, Teotitlán, *Conzatti 4111* (NY, US); near Cerro Zempoaltepetl, SW. slopes near Tlahuitoltepec, *Hallberg 953* (DUKE, ENCB, US); near Talea, *Hartweg 482* (K, NY, P); Patio de Arena, high pt. of trail from Zacatepec to Tamazulapán, *Leonard 3931* (NCU); La Esperanza, Comaltepec, Ixtlán, *MacDougall s.n.,* 18 April 1970 (NY); W. of Santa Maria Chisme, lat. 17°17′, long. 95°43′, *Schultes 500* (NY); between Villa Alta and Tonaguilla, lat. 17°19′, long. 96°08′, *Schultes 599* (NY); near San Pedro Teutila, lat. 18°00′, long. 96°42′, *Schultes 753a* (NY). CHIAPAS: 4 mi. N. of Jitotol, *Breedlove 8989* (ENCB, F, US); Lago de Monte Belle, 25 mi. E. of La Trinitaria, *Breedlove 9683* (F, NY); Los Lagos, 3 mi. NW. of Rancho San José, *Carlson 1784* (F, UC); 3 km. NW. of Pueblo Nuevo Solistahuacán, *Zuill 126* (ENCB).

Lyonia squamulosa is very closely related to *L. ferruginea* and *L. fruticosa* of the southeastern United States (see TABLE 11). It is clearly separated from *L. fruticosa* by the usual lack of unicellular hairs and the more or less persistent peltate scales on the abaxial leaf surface, the usually shorter and more or less subglobose capsules, and the lower frequency of plants having the leaves strongly reduced in size toward the branch apices. *Lyonia squamulosa* can be differentiated from *L. ferruginea* by the usual lack of unicellular hairs on the abaxial leaf surfaces, the plane or only slightly revolute leaf margins, the lack of noticeable depression of the major leaf veins, and the usually shorter, subglobose capsules. *Lyonia squamulosa* also has a tendency to have darker orange or brown peltate scales, and its leaves are more often elliptic or ovate.

Lyonia squamulosa is extremely variable in leaf shape and size, apex type, degree of reduction in leaf size toward branch apices, and pubescence. Some plants have large, elliptic leaves with acute to acuminate apices, while others have small, more or less obovate ones with rounded to acute apices (the former superficially resemble *L. ferruginea,* the latter *L. fruticosa*). However, all sorts of intermediate individuals occur, and even within single populations a wide variability in leaf shape and size is evident (e.g., *Pringle 13096*). This variability has led to much taxonomic confusion, beginning with Martens & Galeotti, who described the species in 1842. They reported both *L. squamulosa* and *L. ferruginea* from Mexico, calling plants with large, more or less elliptic leaves *L. squamulosa* (and comparing them to *L. jamaicensis*) and identifying those with smaller, obovate leaves as *L. ferruginea.* (They were evidently following the nomenclature of Nuttall, 1818). It seems impossible to separate two such groups of Mexican plants satisfactorily since there

is a continuous range of variation between them, and in many respects the characters themselves show a reticulate pattern of variation within the taxon as a whole. Although most specimens lack unicellular hairs on the abaxial leaf surfaces, a few (especially those from San Luis Potosí—see, for example, *Galeotti 1849* (F, GH, P, NY, US); *Schaffner 486* (NY); *Rzedowski 6100* (ENCB); *Parry & Palmer 566* (F, NY)) show a very slight to dense covering of such hairs. These specimens can sometimes be confused with *L. fruticosa*. Strongly revolute leaves, another unusual character in *L. squamulosa*, are present on *Rzedowski 5451*, also collected in San Luis Potosí.

Although this taxon has variously been included under *Lyonia ferruginea* (cf. Sargent, 1893; Long & Lakela, 1971) or accepted as a distinct species (with reservations—Standley, 1924), I believe that to include it in either *L. ferruginea* or *L. fruticosa* would completely destroy the consistency of characters upon which these taxa are based. The differences between these three species are of an order of magnitude similar to those separating many species in the related West Indian taxa, and the characters (e.g., presence or absence of unicellular hairs on abaxial leaf surface, capsule shape and size, depression of secondary veins of leaf, degree of revolution of leaf margin, persistence and structure of peltate scales, habit) are of a similar nature.

34. **Lyonia ferruginea** (Walter) Nutt. Gen. N. Am. Pl. **1:** 266. 1818.

Andromeda ferruginea Walter, Fl. Carolin. 138. 1788. *Cassandra ferruginea* (Walter) Niedz. Bot. Jahrb. **11:** 146, 148, 224. 1889. *Xolisma ferruginea* (Walter) Heller, Catal. N. Am. Pl. 6. 1898. TYPE: the material used by Thomas Walter in describing this species was probably collected in S. Carolina and/or Georgia by John Fraser in late 1786, or 1787. Walter's own herbarium was early destroyed, but because it is probable that *Andromeda ferruginea* Walter was described from Fraser's material, a specimen collected by Fraser in "Georgia" found in de Candolle's herbarium (P-DC (IDC Herb. genevense 1373: I. 7!)) is here selected as the lectotype.

Andromeda ferruginea Walter var. *arborescens* Michaux, Fl. Bor. Am. **1:** 252. 1803. *Lyonia ferruginea* (Walter) Nutt. var. *arborescens* (Michaux) Rehder in Bailey, Cycl. Am. Hort. **3:** 960. 1900. TYPE: St. Augustine [Florida], *A. Michaux* (lectotype, P-MICHX (IDC 6211. 57: II. 4!)).

Andromeda rigida Pursh, Fl. Am. Sept. 292. 1814. *Lyonia rigida* (Pursh) Nutt. Gen. N. Am. Pl. **1:** 266. 1818. TYPE: "in barren sandy woods: Carolina to Florida" (not seen).

Evergreen, laxly branched or spreading shrub or small tree to 5(–10) meters tall, usually from underground woody burl or swelling, spreading vegetatively by short, horizontal, underground rhizomes, with brownish to gray, longitudinally furrowed bark. Twigs slightly angled, slender, ± sparsely lepidote, otherwise usually sparsely to densely pubescent. Buds ovoid, 1–2.5 by 1–2 mm. Leaf blades elliptic to obovate or ovate, 1–9 by 0.5–4.5 cm., those of branch apices similar to or only slightly smaller than those borne on

lower portion of branches, flat to strongly recurved, coriaceous, ca. 0.17–0.26 mm. thick; apex acute or obtuse to acuminate, or less commonly rounded or truncate; base attenuate to narrowly or widely cuneate; margin usually revolute, sometimes strongly so, distal portion entire to undulate, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales quickly deciduous, slightly to densely pubescent on midvein, especially proximal portion, the 3° and higher order veins obscure to slightly visible, the midvein usually depressed, the 2° veins usually at least slightly depressed; abaxial surface densely lepidote, otherwise usually densely (occasionally only sparsely) pubescent, the 3° and higher order veins ± flat or nearly so, obscure to very slightly and laxly reticulate, the 2° veins slightly raised and visible; scales rust colored, sometimes becoming whitish with age, often of 2 sizes (large, irregular to erose, to ca. 0.3 mm. in diameter, and smaller, more nearly entire, ca. 0.08–12 mm. in diameter), at least smaller ones persistent; petiole 2–9 mm. long, lepidote, otherwise ± adaxially pubescent. Flower buds above or intermixed with vegetative buds on branches (or growth-flush) of previous year; inflorescences fasciculate, 1- to 10-flowered. Pedicels clearly articulated with calyx, slender, 4–14 mm. long, lepidote, otherwise glabrous or sparsely pubescent; bracteoles subopposite, basal or nearly so, narrowly triangular, 0.9–1.5 mm. long; bracts to ca. 2 mm. long. Flowers 5- (or 6-)merous; calyx lobes triangular, with acuminate apices, 1–2 by 0.5–1.2 mm., the adaxial side glabrous or more frequently sparsely pubescent, especially near apex or margins, the abaxial side lepidote, otherwise usually glabrous; corolla urceolate, 2–4 by 2–4 mm., white, abaxially sparsely lepidote; filaments roughened, 1–2.3 mm. long, unappendaged or with minute spurs near anther-filament junction, anthers 0.8–1.2 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to ellipsoid, 3–6 by 3–4.5 mm., sparsely lepidote, otherwise sparsely to densely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves; seeds 2–3.5 mm. long. (FIGURES 59, 60; see also Ventenat (1804), Sargent (1893), Harrar & Harrar (1946), West & Arnold (1956), Wood (1961), Kurz, Godfrey, & Wagner (1962), Lakela & Wunderlin (1980).)

DISTRIBUTION AND ECOLOGY. North America, Coastal Plain, Florida north to South Carolina (MAP 31). Chiefly in *Quercus* and/or *Pinus* forests, thickets, evergreen scrub (*Quercus geminata, Q. myrtifolia, Q. chapmanii*) or hammocks; usually well-drained soils. Flowering March and April.

COMMON NAMES. Staggerbush, cudgel-wood, poor-grub, crooked-wood.

REPRESENTATIVE SPECIMENS. **South Carolina.** BEAUFORT CO.: near Bluffton, *Mellichamp s.n.*, 1873 (NY); on Rt. 46 2 mi. S. of Bluffton, *Judd 320* (GH, MSC). JASPER CO.: ca. 6 mi. S. of Hardeeville, *Ahles 10309* (NCU). **Georgia:** BACON CO.: 7.5 mi. E. of Alma, *Bozeman 4471* (NCU). BERRIEN CO.: 6.1 mi. NNE. of Nashville, *Faircloth 2142* (NCU). CAMDEN CO.: S. end of Cumberland Is., *Judd 1699* (A, MSC). CHATHAM CO.: 5.5 mi. S. of Victory Drive, Savannah, *Coker s.n.*, 27 March 1948 (NCU). COFFEE CO.: near Gaskins Spring, hammock of Seventeen Mile Creek, *Harper 2047* (A, GH, NY, US). EFFINGHAM CO.: ca.

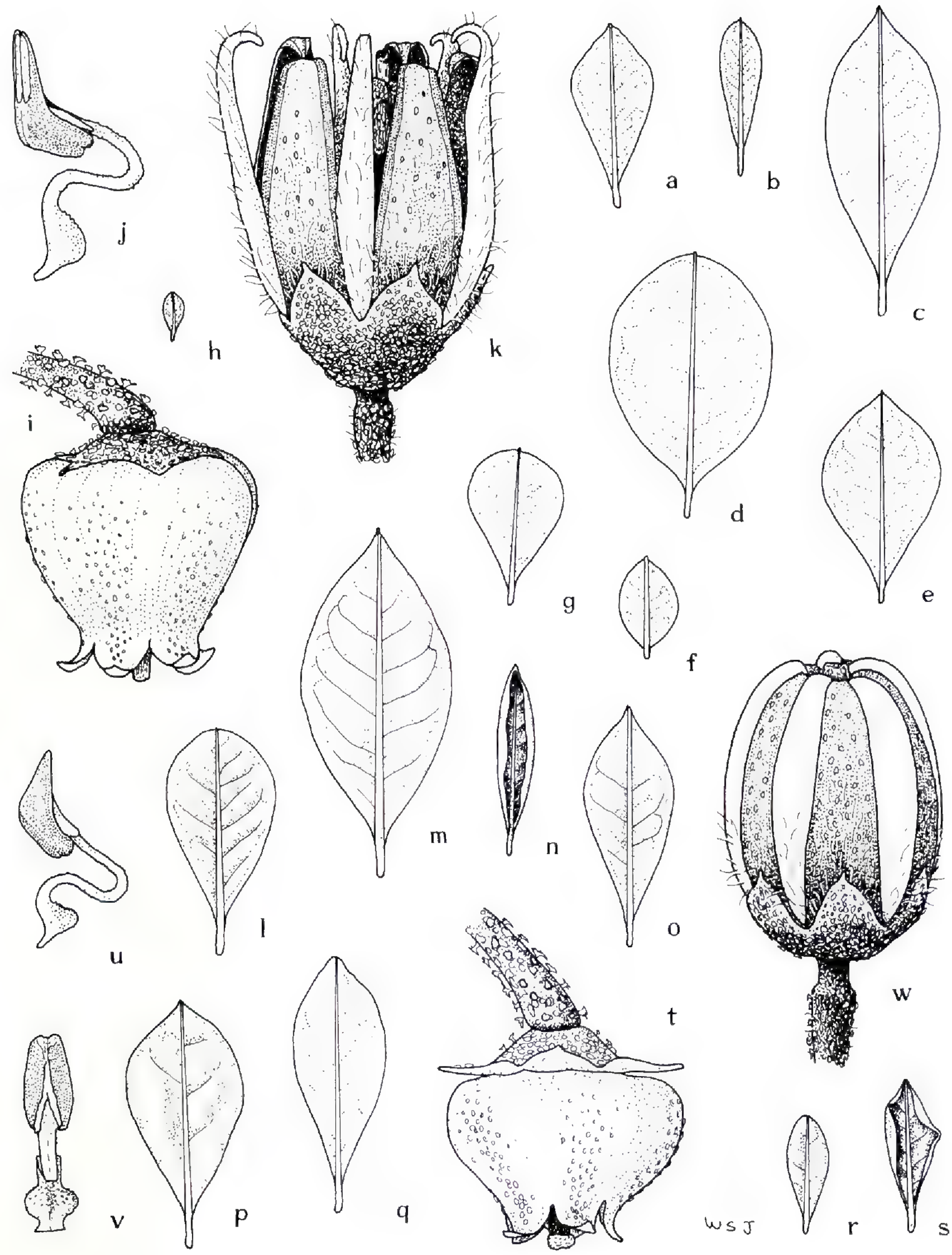
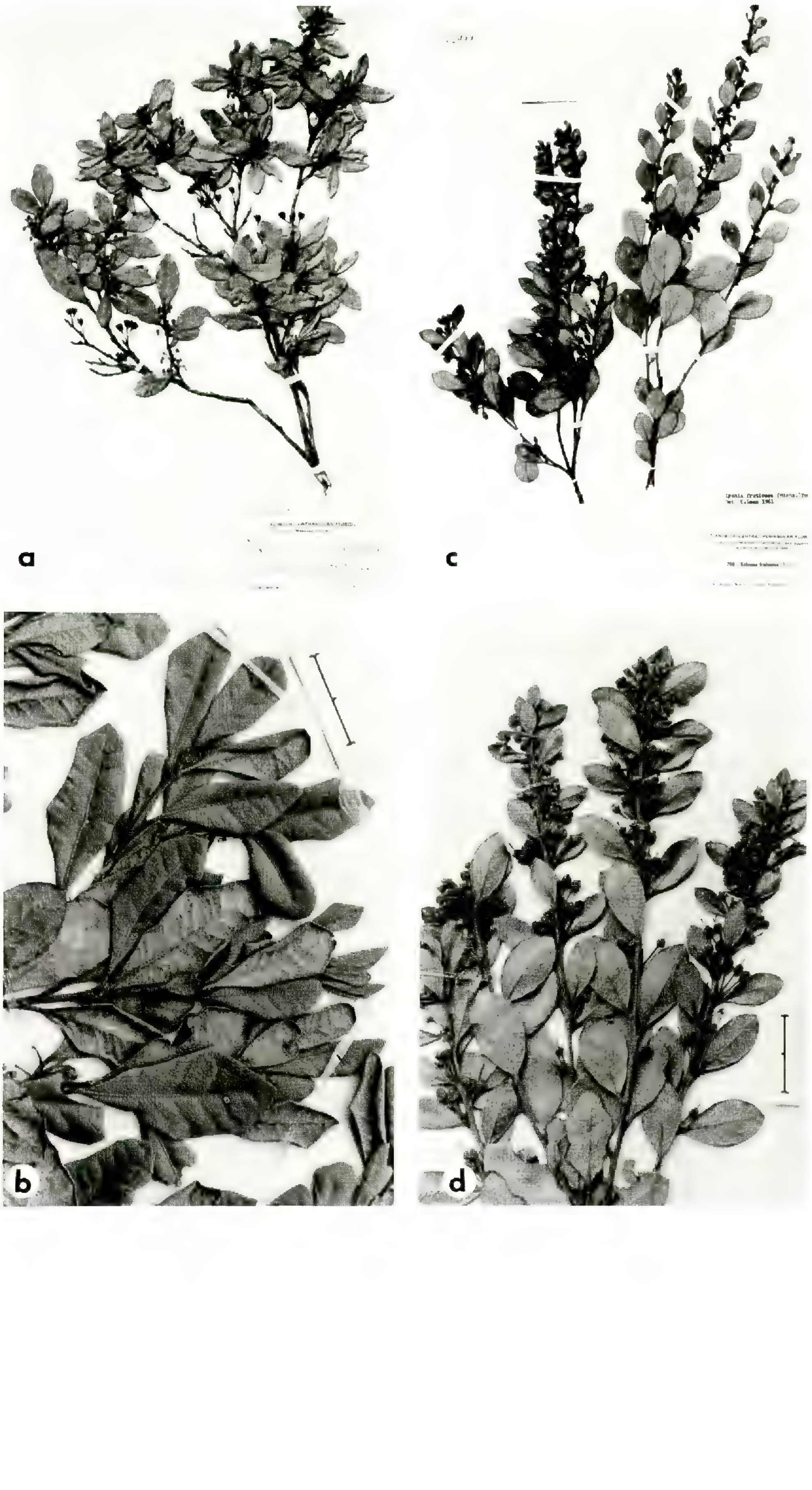


FIGURE 59. a–k, *Lyonia fruticosa:* a–h, leaves, × .5; i, flower, × 6; j, stamen, × 12.5; k, capsule, × 6. l–w, *L. ferruginea:* l–s, leaves, × .5; t, flower, × 6; u, v, stamens, × 12.5; w, capsule, × 6.

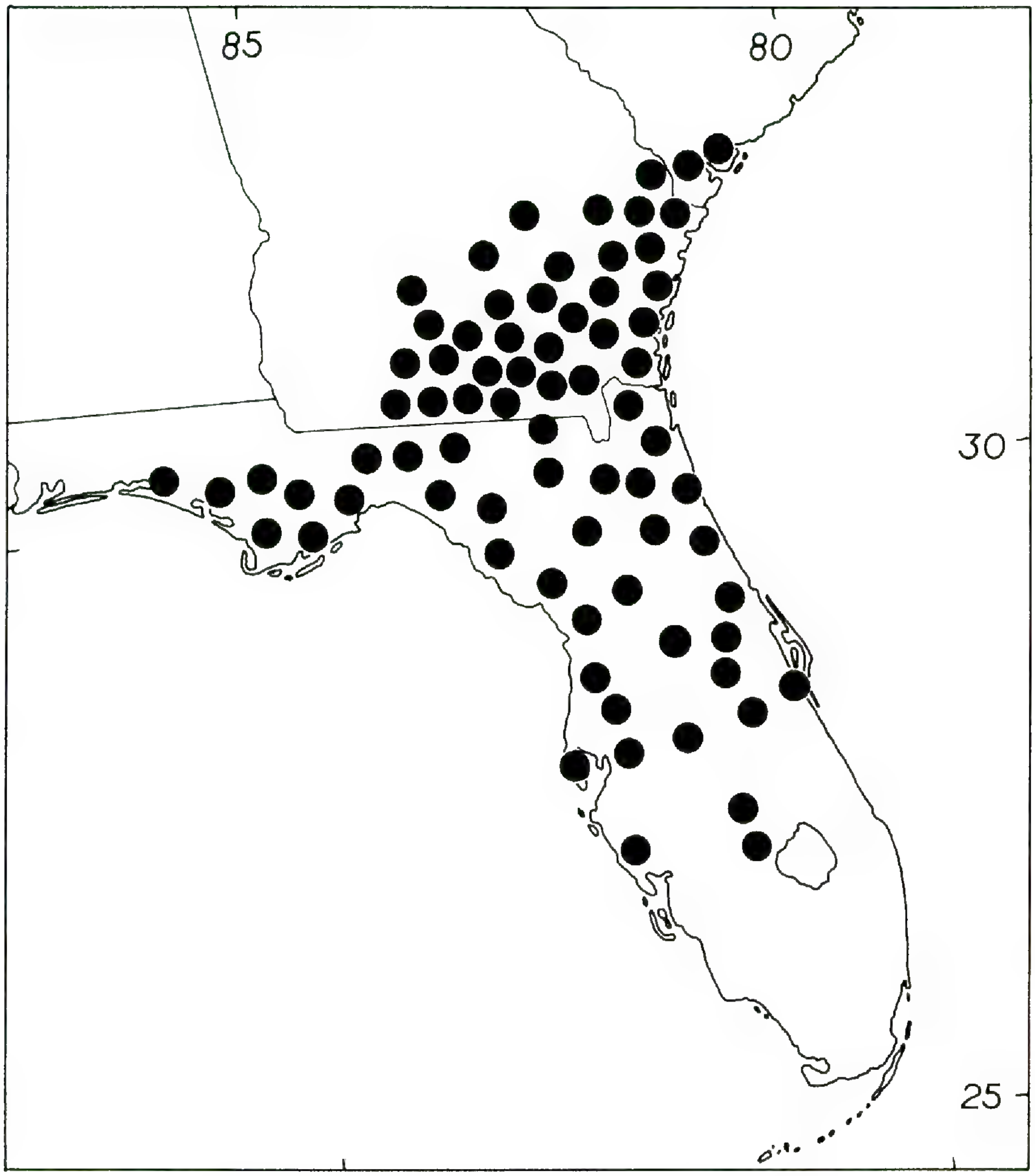

a
c
b
d

3 mi. S. of Stillwell, *Bozeman 4073* (NCU). EVANS CO.: 3.8 mi. NW. of Claxton, *Duncan 15107* (NCU, TEX). GLYNN CO.: Jekyll Is., *Judd 300* (A, MSC). LIBERTY CO.: E. of Hinesville on U. S. 82, *Judd 322* (GH, MSC). LOWNDES CO.: 12.6 mi. NNE. of Valdosta, *Faircloth 3705* (NCU). MONTGOMERY CO.: Co. rd. S-1125, 0.4 mi. E. of Oconee R., *Bozeman 5742* (NCU). TELFAIR CO.: 4.7 mi. W. of McRae, *Dress et al. 721* (GA). THOMAS CO.: 8.3 mi. NE. of Thomasville, *Faircloth 2491* (NCU). TURNER CO.: 4.1 mi. ENE. of Ashburn, *Faircloth 4402* (NCU). WARE CO.: near Suwannee Lake, *Harper 17* (NY). **Florida.** ALACHUA CO.: 7 mi. NE. of Gainesville, *Anderson 37* (FLAS). BAY CO.: 5 mi. N. of Lynn Haven, *Lazor 5009* (FSU). BREVARD CO.: N. of Cocoa, *Rhodes 8305* (A). CALHOUN CO.: 3 mi. W. of Blountstown, *Coker s.n.*, 26 Feb. 1946 (NCU). COLUMBIA CO.: bluff of Sante Fe R., NE. of High Springs, *Godfrey 52847* (DUKE, FSU, GH, MISSA, NCU, NY). DUVAL CO.: vic. of Mayport, *Godfrey & Reinert 61199* (FSU). FRANKLIN CO.: St. Theresa, *Griscom 21596* (GH). GULF CO.: near Wewahitchka, *Demaree 50636* (NCU). HIGHLANDS CO.: near Lake Placid, *Demaree 50250* (FSU, NCU). LAFAYETTE CO.: 4.5 mi. N. of Day, *Duncan 18240* (GA). LAKE CO.: near Eustis, *Nash 17* (A, MSC, NY, US). LEON CO.: near Lake Bradford, *Godfrey 57997* (FSU). LEVY CO.: Cedar Key, *Godfrey 56607* (DUKE, FSU, GH). MARION CO.: Ocala Natl. Forest, *Perry 1643* (DUKE). ORANGE CO.: near Orlando, *Palmer 38306* (A, US). PASCO CO.: near Jessamine, *Barnhart 2540* (NY). PINELLAS CO.: near Dunedin, *Tracy 6648* (GH, MSC). POLK CO.: ca. 2 mi. NE. of Lakeland, *Ford et al. 2440* (NCU). TAYLOR CO.: between Buckville and Perry, *Godfrey 53855* (DUKE, FSU, GH, MISSA, NY). VOLUSIA CO.: near Daytona, *Small & DeWinkeler 9423* (NY).

Lyonia ferruginea is very closely related to *L. fruticosa* and *L. squamulosa*. The characters most useful in differentiating these three species are presented in TABLE 11 and are discussed below. As can be seen from this table, *L. ferruginea* is quite distinct from both *L. fruticosa* and *L. squamulosa*, since these taxa are separated by several consistent differences in phenology, habit, leaf morphology, indumentum, and flower and/or fruit morphology. In addition, very few plants appearing to be intermediate have been discovered. However, these species have often been confused, misunderstood, and misidentified.

There is a long tradition, beginning with Michaux (1803), of recognizing *Lyonia ferruginea*, *L. fruticosa*, and *L. squamulosa* as distinct taxa. Michaux treated *L. ferruginea* and *L. fruticosa* as two varieties of a more inclusive *Andromeda ferruginea*, calling the former *A. ferruginea* var. *arborescens* and the latter *A. ferruginea* var. *fruticosa*, and giving as distinguishing characters habit, degree of revolution of the leaf margin, curvature of the leaf blade,

FIGURE 60. a, b, *Lyonia ferruginea:* a, representative specimen (*Griscom 21596*, GH); b, leaves (*Brass 14619*, GH), note leaves not reduced in size toward branch tips and with depressed secondary veins. c, d, *L. fruticosa:* c, representative specimen (*Nash 700*, MSC), note rigidly ascending branches with leaves reduced near tips; d, leaves (*Lakela 25027*, GH), note secondary veins not depressed and leaves less ferrugineous on abaxial surfaces. Scale in b, d = 2 cm.



MAP 31. Distribution of *Lyonia ferruginea*.

prominence of leaf venation, amount of crowding of the leaves on the stem, and differences in flowering time. Asa Gray (1878) also considered these two taxa as varietally distinct, pointing out that the leaves of *L. ferruginea* are narrower (sic) and less reticulate veined, while those of *L. fruticosa* are mostly cuneate-obovate or rhomboid and conspicuously reticulate. Elliott (1817), Nuttall (1818), Nash (1895), Small (1913, 1914, 1933), Lems (1962, and unpubl. notes), and Long and Lakela (1971) all considered *L. fruticosa* and *L. ferruginea* to be specifically distinct. Nash (1895) first pointed out that *L. fruticosa* has a "stricter habit" (i.e., its branches are more rigidly ascending) than *L. ferruginea*, and Small (1913, 1914) first mentioned that in *L. ferruginea* the leaves are "not much reduced toward the ends of the

branchlets," in contrast to the usually conspicuously reduced leaves of *L. fruticosa*. He also noted that *L. ferruginea* tends to have slightly smaller flowers (a character later used by Long & Lakela (1971) to key out these taxa, although probably unwisely, since the range of overlap is great). In addition, Lems (unpubl. notes) suggested that *L. ferruginea* has less densely tomentose leaves, smaller flower clusters, narrower and longer leaves, and shoots in which growth terminates after flowering. However, although *L. ferruginea* does tend to have longer leaves than *L. fruticosa*, there is a wide range of overlap between the two taxa in this character; *Lyonia ferruginea* is quite as pubescent as *L. fruticosa*, but its unicellular hairs are more frequently obscured by its persistent peltate scales; and no significant difference could be found in the number of flowers per inflorescence (pers. obs.). Other characters helpful in identifying these taxa are listed in TABLE 11. *Lyonia squamulosa*, in contrast to *L. ferruginea* and *L. fruticosa*, has been considered by relatively few botanists. It was not described until 1842, when it was reported by Martens and Galeotti, who considered it to be closely related to *L. ferruginea*. Small (1914) separated *L. squamulosa* from *L. fruticosa* and *L. ferruginea* by its subglobose capsules, and Standley (1924, p. 1092), although he recognized it at the specific level, said, "The Mexican plant differs [from *L. ferruginea*] only in its slightly shorter capsules and it is doubtful whether it represents a distinct species." Actually, this taxon can also be distinguished by the usual lack of unicellular hairs and by the more or less persistent ferrugineous scales on its abaxial leaf surfaces. However, authors such as Radford *et al.* (1968) and Sargent (1893) have considered these three taxa to be conspecific. Part of the difficulty involving these species is that the characters that separate them are either best seen in the field or difficult to see at all without the aid of a high-powered (at least 30×) dissecting microscope. For example, the curvature of the leaf blade, the amount of marginal revolution, and the depression of the secondary veins—all very useful characters—are frequently seriously distorted in pressed and dried herbarium specimens. The habit and branching pattern are very often not given on the specimen label, further increasing difficulties in identification. In some cases it is thus necessary, when dealing with pressed material, to resort to less useful or more difficult to observe characters. A final source of difficulty is that, like all lyonias, these species are quite variable, and this variability contains both genetic and environmental components. For example, in *L. ferruginea*, the leaves from some plants are only ca. 2–3 cm. long and are so extremely recurved that they are nearly rolled into a cylinder, while those from other plants are large (to ca. 6 cm.), more or less flat, and only slightly revolute (see FIGURE 59).

Lyonia ferruginea is, of course, geographically isolated from *L. squamulosa* and is isolated from *L. fruticosa* by its ecology and earlier flowering period. Differences in flowering time between *L. ferruginea* and *L. fruticosa* were observed by Michaux (1803), Pursh (1814), and Nash (1895), but Elliott (1817, p. 489) wrote that "the different periods of flowering, as they were determined by Michaux from cultivation, mark a difference of habit; yet in the woods

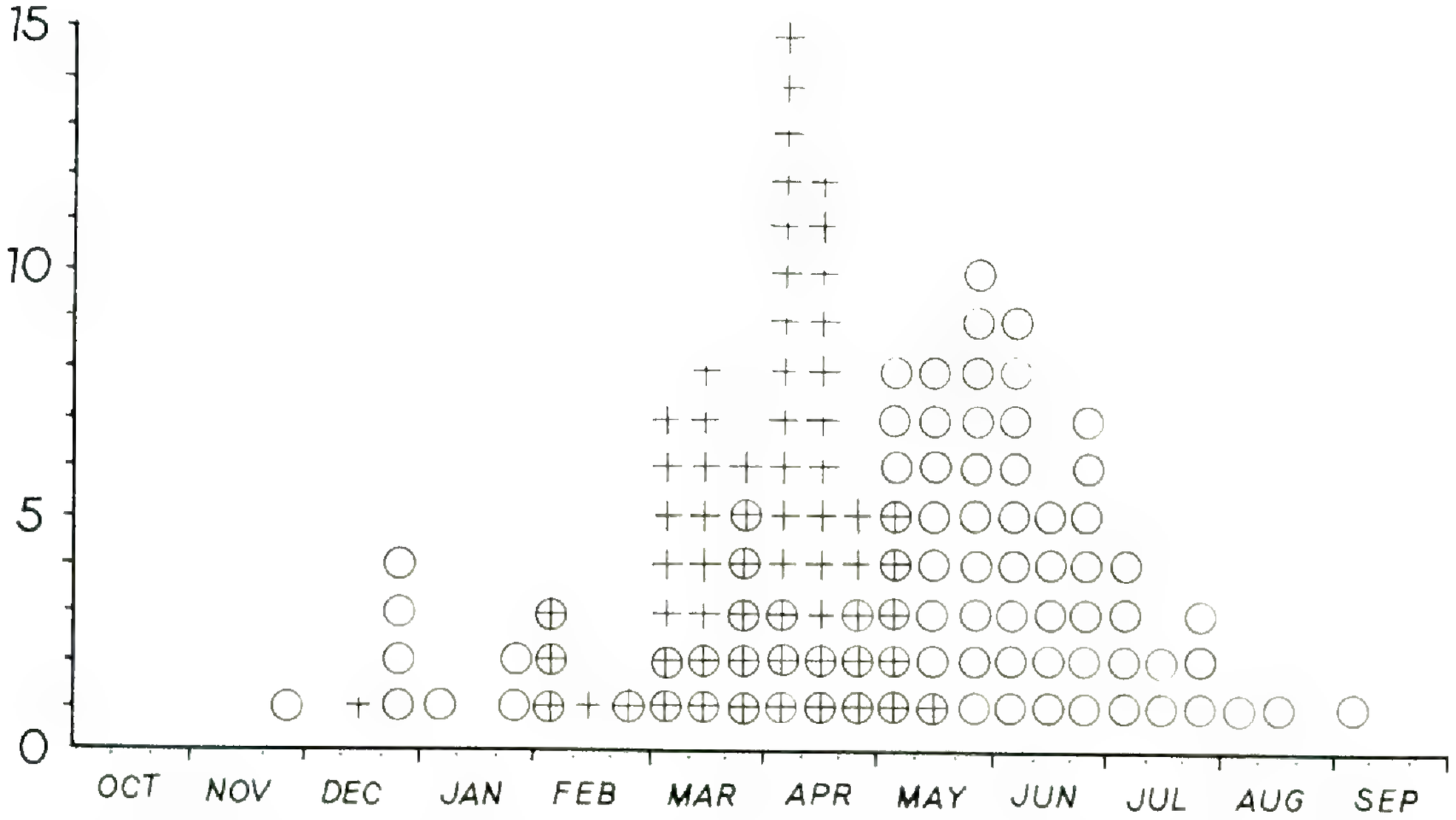


FIGURE 61. Comparison of flowering periods of *Lyonia fruticosa* and *L. ferruginea*, based upon herbarium specimens (o = *L. fruticosa*; + = *L. ferruginea*; vertical axis = no. of specimens; horizontal axis = flowering time). Amount of overlap in blooming time in any one place actually much less than indicated since figure based upon herbarium specimens from throughout range of species.

[i.e., in nature] this difference is not obvious, but there appears to be a constant succession of flowers from April to June." It does appear that there is considerable overlap in flowering times, especially in southern Florida, but *L. ferruginea* begins its most intensive blooming period significantly earlier than *L. fruticosa* (see FIGURE 61). Field observations in southeastern Georgia and northern to north-central Florida confirm Michaux's observation since in any one locality, *L. ferruginea* begins to bloom significantly before *L. fruticosa* and has essentially completed flowering by the time *L. fruticosa* is in its peak bloom. Michaux's experiment has also been repeated with similar results: in plants grown under uniform greenhouse conditions in East Lansing, Michigan, and in Cambridge, Massachusetts, the peak of flowering of *L. ferruginea* was always approximately one and one-half to two months earlier than that of *L. fruticosa*. This difference in blooming time results from the fact that in *L. ferruginea* the flowers are nearly always restricted to the previous year's branches (or branches of the previous growth-flush), while in *L. fruticosa* flowers are most frequent on the present year's branchlets (or branches of the present growth-flush) although a few flowers are also sometimes borne on branches of the previous year.

To judge from the author's rather limited collecting experience, *Lyonia ferruginea* seems to be more common in oak or oak and pine forests, thickets, or scrub (on well-drained sands), or in hammocks with acid humus. It occurs in both shaded and very sunny habitats (with its leaves varying from large

and more or less flat in shaded situations to often small and quite revolute in sunny areas). In contrast, *L. fruticosa* abounds in the sunny, open, often poorly drained, pine-palmetto flatwoods or in scrub vegetation dominating areas where the pines have been cut. *Lyonia ferruginea* and *L. fruticosa* can occasionally be found growing together, but plants showing intermediate characters have only very rarely been found (pers. obs.).

Lyonia ferruginea, along with *L. squamulosa* and *L. fruticosa*, characteristically forms large, elongated, woody burls or underground swellings reaching ca. 1.5 meters in length; these are capable of repeated sprouting, especially after fire and/or cutting, and often produce horizontal rhizomes. The rhizome network of *L. ferruginea* is usually less extensive than that of *L. fruticosa*.

Seedlings tend to have very small, narrow leaves that often lack or are only sparsely covered with unicellular hairs beneath. The leaves acquire their normal dense pubescence as the plant matures. Seedlings are most common in open, sunny, often-disturbed areas. Rapidly growing young shoots of *Lyonia ferruginea* tend to be rigidly ascending and thus superficially resemble *L. fruticosa*.

The typification of the name *Andromeda ferruginea* Walter has involved several problems. Thomas Walter's *Flora Caroliniana* (1788) described about 1000 species distributed among 435 genera; this classic work was based upon studies of specimens collected by Walter within a radius of 50 miles from his plantation, located at the southern edge of the great swamp bordering the Santee River in St. John's Parish (present-day Berkeley Co.), South Carolina, and upon material brought to him by John Fraser. Fraser had met Walter soon after his arrival in Charleston, South Carolina, on September 20, 1786, on a trip to the "southern parts of the American provinces, in order to form a complete botanical collection of the native plants of that part of the continent" (Fraser, 1789, p. 3; see also discussion in Maxon, 1936). Fraser resided in South Carolina and Georgia for 19 months before returning to England in March, 1788, taking with him the manuscript of Walter's *Flora* and his own collections (comprising ca. 30,000 dried specimens and many living plants). At a later date, some fragments were selected from this material, perhaps by Fraser's son, and designated the "Walter Herbarium" (now at the British Museum (Natural History)) (see Ward, 1977). Fraser, himself (1789, p. 4), stated:

> The botanical descriptions of many of the plants which I found, are contained in the FLORA CAROLINIANA; with the author of which, the late Mr. WALTER, I became acquainted soon after my arrival in Carolina. He had collected, when I went into that country, plants which afforded him six hundred and forty descriptions. I increased his work, by the specimens I produced to him, to one thousand and sixty; amongst which are upwards of *two hundred new species*, and *thirty new genera;* of all which, as well as the other plants in the FLORA, I have now dried specimens in my possession, and many valuable living plants.

Lyonia ferruginea must have been one of the plants supplied to Walter by Fraser, since neither *L. ferruginea* nor *L. fruticosa* occurs anywhere in the

vicinity of Walter's plantation (in South Carolina they are limited to the two southernmost counties, Beaufort and Jasper, where they are very rare). Fraser (1789, p. 4) traveled from "the south boundaries of Georgia to the northward of Carolina, a course of near six hundred miles." He became acquainted with Michaux in Charleston, and the two collected together until "Mr. Michaux had the misfortune to have his horses stolen from him in the woods between Savannah and Augusta" (Fraser, 1789, p. 3; but see Michaux's version in Ward, 1977). It is very probable that Fraser, in his travels with Michaux, collected several specimens of *L. ferruginea* and *L. fruticosa* that were later (sometime in 1787) presented to Walter for description. Walter's description (1788, p. 138) "foliis rotundatus margine revolutis, subtus ferrugineis" is not complete enough for exact determination, but it fits *L. ferruginea* better than *L. fruticosa:* the former has markedly revolute leaves with a dense and persistent covering of ferrugineous scales beneath, while the latter has usually nonrevolute leaves with deciduous scales. It is likely that Walter, with very few specimens available to him, included both *L. ferruginea* and *L. fruticosa* in his *Andromeda ferruginea,* since specimens of *L. ferruginea* (see IDC, Herb. genevense 1373: I. 7) and of *L. fruticosa* (see IDC, Herb. genevense 1373: I. 6, in part) collected by Fraser in his excursion through South Carolina and Georgia are known. If Walter's name (1788) includes two elements, as seems likely, it is necessary to select a specimen of one or the other element as the lectotype. Because Walter's description seems to fit *L. ferruginea* better, and because Walter's name has been used since 1803 in this sense, I have chosen to lectotypify *A. ferruginea* Walter by the revolute-leaved element (i.e., *L. ferruginea,* as considered here). Since Walter's own specimens have surely been lost, I have lectotypfied this name by selecting a specimen collected by Fraser (IDC, Herb. genevense 1373: I. 7, at P-DC) that agrees well with Walter's description and that is also likely to have been seen by Walter. Among the fragments of Fraser's material presently designated as the "Walter Herbarium" is one labeled "*Andromeda ferruginea*" (photos at GH and FLAS; see discussion in Blake (1915), Maxon (1936), Fernald & Schubert (1948)), which is actually *L. fruticosa.* This "herbarium" is rather poor, with many specimens missing or represented by mere fragments. The fragment does not agree well with Walter's description. I am thus not considering this specimen as the type of Walter's *Andromeda ferruginea.* (Pursh was the first botanist to study the fragments known as the "Walter Herbarium." The specimen mentioned above probably led him to use the name *Andromeda ferruginea* for what is now known as *Lyonia fruticosa;* he then provided the name *A. rigida* for what Michaux had called *A. ferruginea* var. *arborescens* and what is here treated as *L. ferruginea.* Nuttall followed Pursh's interpretation.)

35. **Lyonia fruticosa** (Michaux) G. S. Torrey in Robinson, Proc. Am. Acad. **51:** 527. 1916.

Andromeda ferruginea Walter var. *fruticosa* Michaux, Fl. Bor. Am. **1:** 252. 1803. *Xolisma fruticosa* (Michaux) Nash, Bull. Torrey Bot. Club

22: 153. 1895. *Lyonia ferruginea* (Walter) Nutt. var. *fruticosa* (Michaux) Rehder in Bailey, Cycl. Am. Hort. **3:** 960. 1900. TYPE: "Georgia meridionale, Cumberland Island," *A. Michaux* (lectotype, P-MICHX (IDC 6211. 57: II. 1!)).

Andromeda ferruginea var. *frutescens* Veillard in Duhamel, Traité Arbres Arbustes. ed. 2 (Nouv. Duhamel). 190. [1800–] 1801–1819 (this description probably published in 1803). TYPE: (not seen).

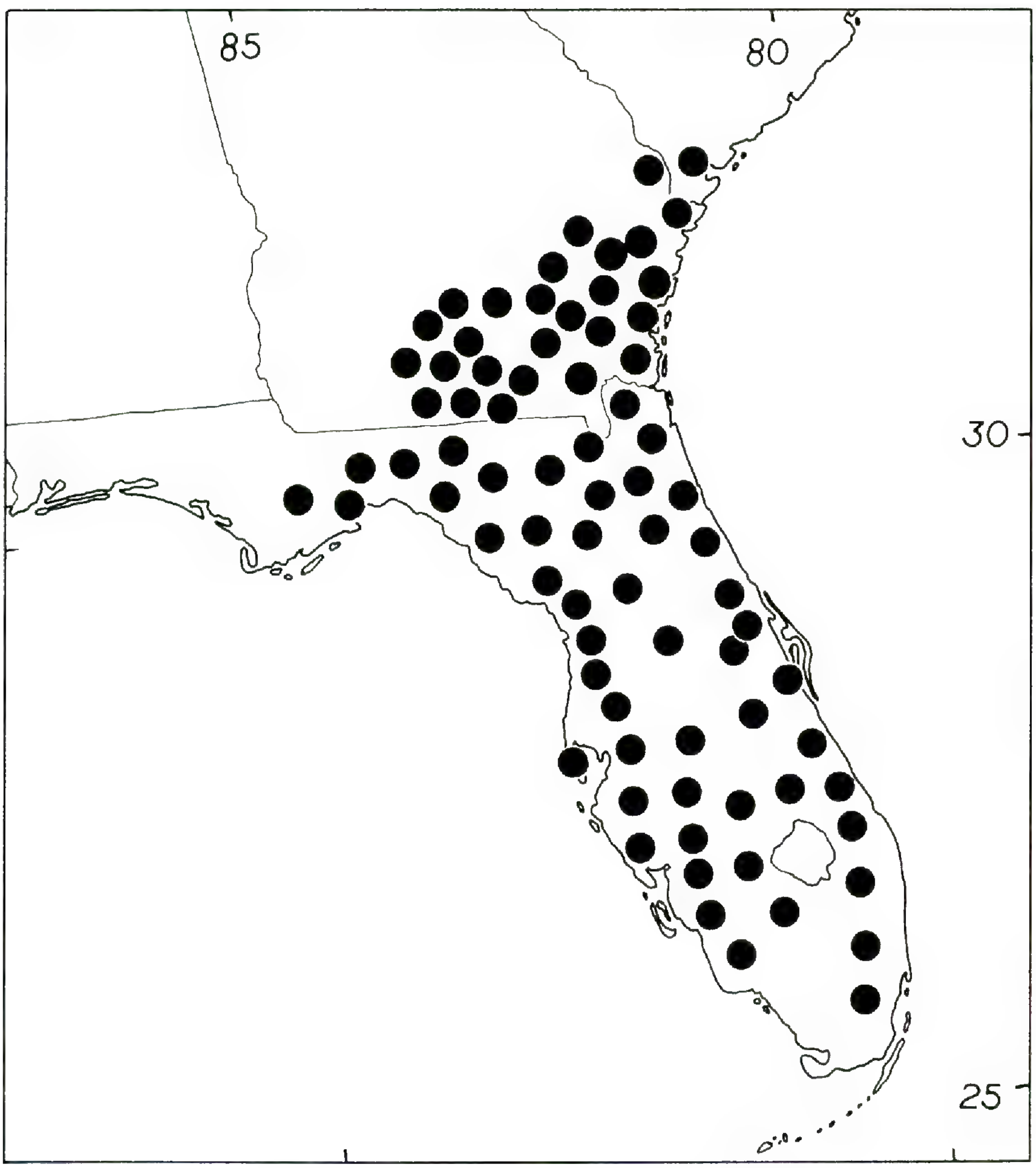
Evergreen, upright shrub to 1.5(–3) meters tall, usually with rigidly ascending branches, from an underground woody burl or swelling, often spreading vegetatively by short, horizontal, underground rhizomes, with grayish, longitudinally furrowed bark. Twigs slightly angled, slender, ± sparsely lepidote, otherwise usually moderately to densely pubescent. Buds ovoid, 1–2.5 by 1–1.5 mm. Leaf blades obovate or less commonly elliptic, 0.5–6 by 0.3–4 cm., usually conspicuously reduced in size toward branch apices, flat to slightly concave (less commonly slightly recurved), coriaceous, ca. 0.17–0.27 mm. thick; apex acute, abruptly acuminate or rounded; base attenuate to narrowly or widely cuneate; margin plane to very slightly revolute, distal portion entire to undulate or rarely very obscurely and irregularly toothed, proximal portion entire; venation brochidodromous, 3° veins ± reticulate; adaxial surface lepidote but scales quickly deciduous, moderately to densely pubescent on midvein, especially proximal portion, occasionally with few hairs on some 2° veins, the 3° and higher order veins usually visible, the midvein usually not depressed, the 2° veins visible, not depressed; abaxial surface densely lepidote when young, becoming very sparsely so with age, otherwise usually densely pubescent (occasionally only sparsely pubescent; rarely glabrous), 3° and higher order veins usually slightly raised and visible; scales rust colored, sometimes becoming whitish with age, deciduous, ca. 0.1–0.25 mm. in diameter, erose to nearly entire; petiole 1–7.5 mm. long, lepidote, otherwise adaxially pubescent. Flower buds above or intermixed with vegetative buds, often densely clustered in upper portions of branches (i.e., that part of branch with leaves strongly reduced), borne chiefly on growth of present season (or growth-flush); inflorescences fasciculate (to rarely shortly racemose), 1- to 10-flowered. Pedicels clearly articulated with calyx, slender, 3–15 mm. long, lepidote, otherwise pubescent; bracteoles subopposite, basal or nearly so, narrowly triangular, 0.9–2 mm. long; bracts to ca. 2 mm. long, quickly deciduous. Flowers (4- or) 5- (or 6-)merous or in occasional individuals 5- or 6- (or 8-)merous; calyx lobes triangular, with acuminate apices, 1–1.5 by 0.5–1 mm., the adaxial side sparsely to moderately pubescent, especially near apex or margins, the abaxial side lepidote, otherwise usually glabrous; corolla urceolate, 2.5–5 by 2.5–4 mm., white, abaxially sparsely lepidote; filaments roughened, 1–2.5 mm. long, unappendaged or with minute spurs near anther-filament junction, anthers 0.8–1.5 mm. long; ovary lepidote, otherwise pubescent, placentae ± subapical. Capsule ovoid to ellipsoid, 3–5 by 2.5–4.5 mm., sparsely lepidote, otherwise moderately to densely pubescent, especially near base, the pale, very thick sutures separating as unit from adjacent valves, sometimes with additional pale lines

alternating with and resembling sutures; seeds 1.5–2.5 mm. long. (FIGURES 59, 60; see also Wood (1961).)

DISTRIBUTION AND ECOLOGY. North America, Coastal Plain, Florida to Georgia (very rarely South Carolina) (MAP 32). Chiefly in *Pinus-Serenoa* flatwoods, scrub vegetation, or *Pinus-Quercus* forests; poorly drained soils. Flowering peak May and June (although some plants in flower throughout year, especially in southern Florida).

COMMON NAMES. Stagger-bush, poor grub.

REPRESENTATIVE SPECIMENS. **South Carolina:** without definite locality, *Fraser s.n.* (P-DC (IDC Herb. genevense 1373: I. 6, in part!)); *Bosc s.n.* (P-DC (IDC



MAP 32. Distribution of *Lyonia fruticosa*.

Herb. genevense 1373: I. 6, in part!)). **Georgia.** Appling Co.: 4 mi. NW. of Baxley, *Jones 15103* (DUKE). Bacon Co.: 1.8 mi. E. of Alma, *Duncan 16268* (GA). Berrien Co.: 2 mi. NNW. of Ray City, *Faircloth 1947* (NCU). Brooks Co.: 6 mi. S. of Morven, *Bozeman 4917* (NCU). Camden Co.: ca. 3 mi. W. of St. Marys, *Judd 1733* (MSC). Coffee Co.: 7.6 mi. E. of Douglas, *Duncan 13683* (GA). Colquitt Co.: Indian Creek, 3.3 mi. NW. of Berlin, *Faircloth 2664* (NCU). Cook Co.: 7.5 mi. N. of Sparks, *Judd 267* (MSC). Echols Co.: Tom Creek Swamp, 0.7 mi. N. of Florida St. line, *Bozeman 4660* (NCU). Effingham Co.: 4 mi. N. of Stillwell, *Duncan 15155* (GA). Liberty Co.: 3 mi. SW. of Hinesville, *Wiegand & Manning 2387* (GH). Ware Co.: near Waycross, *Godfrey 50402* (FSU, GH, TEX). **Florida.** Baker Co.: 5 mi. E. of Olustee, *Wiegand & Manning 2389* (GH). Brevard Co.: 10 mi. S. of Melbourne, *Deam 57588* (NY). Collier Co.: Marco Is., *Lakela 30966* (FSU, GH). Columbia Co.: 24.5 mi. N. of Lake City, *Godfrey 63740* (FSU). Dade Co.: Miami, *Tracy 9210* (GH, MSC, TEX, NY, US). Duval Co.: near Mayport, *Godfrey & Reinert 61200* (FSU). Flagler Co.: E. of Bunnell, *West & Arnold s.n.*, 18 April 1940 (FLAS). Gilchrist Co.: ca. 6 mi. E. of Trenton, *Ward et al. 2652* (FLAS, FSU, GH, NCU, US). Hendry Co.: 7 mi. W. of LaBelle, *Baltzell 7986* (FLAS). Highlands Co.: 3.5 mi. S. of Baias Den, *Ray et al. 9802* (NCU). Jefferson Co.: 4 mi. E. of Drifton, *Kral 6422* (FSU, GA, GH). Lake Co.: near Eustis, *Nash 700* (A, MSC, NY, US). Lee Co.: Pine Is., *Tracy 7263* (GH, MSC, NY, US). Levy Co.: 4 mi. N. of Cedar Key, *Godfrey 56618* (DUKE, FSU, GH). Liberty Co.: between Telogia and Sumatra, *Godfrey 62634* (FSU, NY, TEX). Marion Co.: Rte. 40, 2.4 mi. W. of jct. with Rte. 19, *Lems s.n.*, 16 July 1959 (MSC). Palm Beach Co.: 3 mi. E. of Sunshine Pkwy., toward Boca Raton, *McDaniel 9136* (DUKE). Pinellas Co.: 5 mi. S. of Port Richey, *Ray et al. 9989* (FSU, NCU). Polk Co.: near Lake Wales, *Demaree 49436* (FSU). Sarasota Co.: near Phillippe Creek, ca. 3 mi. S. of Sarasota, *Ward 3135* (FLAS, GH, NCU). Taylor Co.: at Steinhatchee, *Godfrey 55953* (FSU, GH, NCU). Wakulla Co.: Apalachicola Natl. Forest, along Rte. 309, between Helen and Lost creeks, *Clewell 1662* (FSU).

This taxon is quite distinct from the closely related and sympatric *Lyonia ferruginea*, and from the geographically isolated *L. squamulosa*. It is easily recognized by its shrubby habit, its rigidly ascending branchlets with more or less conspicuously reduced leaves, its tendency for the flowers to be borne on the newly emerging shoots, its more or less deciduous ferrugineous scales, and its usually densely pubescent and slightly raised-reticulate abaxial leaf surfaces. The morphological differences between these three species are summarized in Table 11 and are discussed, along with possible isolating mechanisms, in more detail under *L. ferruginea*.

Lyonia fruticosa is quite variable in type of leaf apex and in indumentum. Plants with predominantly rounded leaf apices and those with acute or acuminate apices can usually be found in a single population, and often rounded and acute leaves occur together on individual plants. Although most plants are densely pubescent on the abaxial leaf surface, occasional individuals with only a few such hairs (or rarely none at all) can be found.

Even very small shrubs of *Lyonia fruticosa* characteristically have an elongated woody burl just below the soil surface. This structure is capable of repeated sprouting, especially after disturbance or fire. Some of the sprouts

ascend immediately, producing new vertical branches, while others may extend in the soil horizontally for up to a meter before emerging as upright branches. Seedlings or very young plants have small obovate leaves that are often lacking unicellular hairs beneath.

Lyonia fruticosa extends farther south on the Florida peninsula than *L. ferruginea*, but it does not occur as far north as the latter (MAPS 31, 32).

SPECIES EXCLUDED FROM LYONIA

Lyonia arborea (L.) D. Don, Edinburgh New Philos. Jour. **17:** 159. 1834 = **Oxydendrum arboreum** (L.) DC.

Lyonia axillaris (Lam.) K. Koch, Dendrol. **2:** 124. 1872 = **Leucothoë axillaris** (Lam.) D. Don.

Lyonia bracteata (W. W. Sm.) Chun, Sunyatsenia **4:** 253. 1940 = *Vaccinium* sp.

Lyonia calyculata (L.) Reichenb. Fl. German. Excurs. 414. 1830 = **Chamaedaphne calyculata** (L.) Moench.

Lyonia catesbaei (Walter) K. Koch, Dendrol. **2:** 125. 1872 = **Leucothoë axillaris** (Lam.) D. Don.

Lyonia floribunda (Pursh) K. Koch, Dendrol. **2:** 115. 1872 = **Pieris floribunda** (Pursh) Bentham & Hooker.

Lyonia formosa (Wallich) Hand.-Mazz. Symb. Sin. **7:** 790. 1936 = **Pieris formosa** (Wallich) D. Don.

Lyonia grayana (Maxim.) Beiss. in Schelle & Zabel, Handb. Laubh.-Benenn. 392. 1903 = **Leucothoë grayana** Maxim.

Lyonia nana (Maxim.) Makino, Bot. Mag. Tokyo **20:** 85. 1906, *pro. syn.* = **Pieris nana** (Maxim.) Makino.

Lyonia palustris (Pursh) Small, Fl. Miami, 149, 200. 1913 = **Cynanchum palustre** (Pursh) Heller. Small considered this species to be in *Lyonia* Ell., not *Lyonia* Nutt.

Lyonia polita (W. W. Sm. & Jeffrey) Chun, Sunyatsenia **4:** 253. 1940 = **Pieris japonica** (Thunb.) D. Don ex G. Don.

Lyonia popowii (Palibin) Chun, Sunyatsenia **4:** 253. 1940 = **Pieris japonica** (Thunb.) D. Don ex G. Don.

Lyonia populifolia (Lam.) K. Koch, Dendrol. **2:** 123. 1872 = **Agarista populifolia** (Lam.) Judd.

NOMINA AMBIGUA AND NUDA

Andromeda globulifera Gordon in Dermer & Edmonds, Catal. Trees, 4. 1872, *nomen nudum*. This name was occasionally applied to *Lyonia ligustrina* by various early botanists.

Andromeda obovata Raf. Herb. Raf. pt. 3, 57. 1833, *nomen nudum*. Indicated as being from Florida. Asa Gray (1878, p. 32) said that this is a form of *Lyonia lucida* "with smaller and rhombic-obovoid leaves," but there is no way to substantiate this statement.

Andromeda pauciflora Raf. Herb. Raf. pt. 3, 57. 1833, *nomen nudum*. This name probably refers to *Lyonia ligustrina* because Rafinesque indicated that it occurs in "mts. Apalaches" and said that it "belongs to S.G. *Hemiclis* Raf. or *Lyonia* Nuttall." *Lyonia ligustrina* is the only species

of the genus that occurs in the Appalachians.

Andromeda pilulifera Gordon in Dermer & Edmonds, Catal. Trees, 4. 1872, *nomen nudum*. This name has occasionally been applied to *Lyonia ligustrina*.

Andromeda rhomboidalis Veillard in Duhamel, Traité Arbres Arbustes. ed. 2 (Nouv. Duhamel). 192. [1800–]1901–1919 (this description probably published in 1803). TYPE: not seen, and probably destroyed. This name cannot be applied. It probably refers to either *Lyonia ferruginea* or *L. fruticosa*, because the description states that the lower leaf surface is whitish and dusted with a rust color and the range is given as "la Caroline méridionale et la Floride." However, the description is not detailed enough to determine with certainty which of these two closely related species is meant. The following combination exists: *Lyonia rhomboidalis* (Veillard) G. Don, Gen. Syst. **3:** 831. 1834.

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Erratum—On Figure 2, page 74, of Volume 62, Number 1 (January, 1981; Part I of the present article), "*myrtifolia*" should read "*myrtilloides*."

NOTICE

Because of continually increasing production costs, the Editorial Committee of the *Journal of the Arnold Arboretum* is requesting authors to help defray publication expenses. Beginning with manuscripts received and accepted for publication as of March, 1980, a page charge will be levied. Acceptance of manuscripts for the Journal will, however, continue to be based solely on appropriateness and scientific merit, not on an author's ability to meet page costs. Information on page charges and general editorial policies can be obtained from the Managing Editor.

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DICOTYLEDONOUS WOOD FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA. III. CONCLUSIONS

VIRGINIA M. PAGE

THE PRESENT REPORT is the last in a series concerning an assemblage of dicotyledonous woods obtained from Upper Cretaceous marine deposits in central California (Page, 1967, 1968, 1970, 1979, 1980). The specimens were collected from five localities (MAP 1), which have been designated as 1, 2a, 2b, 3, and 4. Localities 1, 2a, and 2b lie in the foothills of the Diablo Range immediately to the west of the town of Patterson in Stanislaus County. Locality 2b is about three-eighths of a mile south of locality 2a. The two sites lie on strike and are essentially time equivalent (J. Stein, pers. comm.). Locality 1 is about two and one-quarter miles northwest of locality 2b and is slightly oblique to regional strike. Chmura (1973) places locality 1 stratigraphically above 2a (and therefore above 2b as well) and estimates the stratigraphic distance between them to be about 1200 feet (365 m.). All three localities are regarded by most workers as Maastrichtian in age. Locality 3 is an exposure of the Sites Formation along Cache Creek in Yolo County on the west side of the Sacramento Valley. The age of the formation has been regarded as Coniacian (Douglas, 1969; Pessagno, 1974) or late Turonian (Popenoe *et al.*, 1960). Locality 4 lies west of the Coast Range in an outcrop of the Pigeon Point Formation on the San Mateo County coast one-half mile north of Pigeon Point. Hall *et al.* (1959) and Wentworth (1960) regard the Pigeon Point Formation as Campanian in age. More detailed information about localities 1, 2a, and 2b is presented in Page (1979), and about localities 3 and 4 in Page (1980). Since the last two localities yielded only one specimen each, the following discussion will be devoted almost exclusively to specimens collected from the other three sites.

Because the mode of deposition has some bearing on the interpretation of the fossils, a short summary of pertinent current theories on the sedimentation history of the area in which the fossils were collected is presented here. The Cretaceous of California is present in an almost continuous sequence

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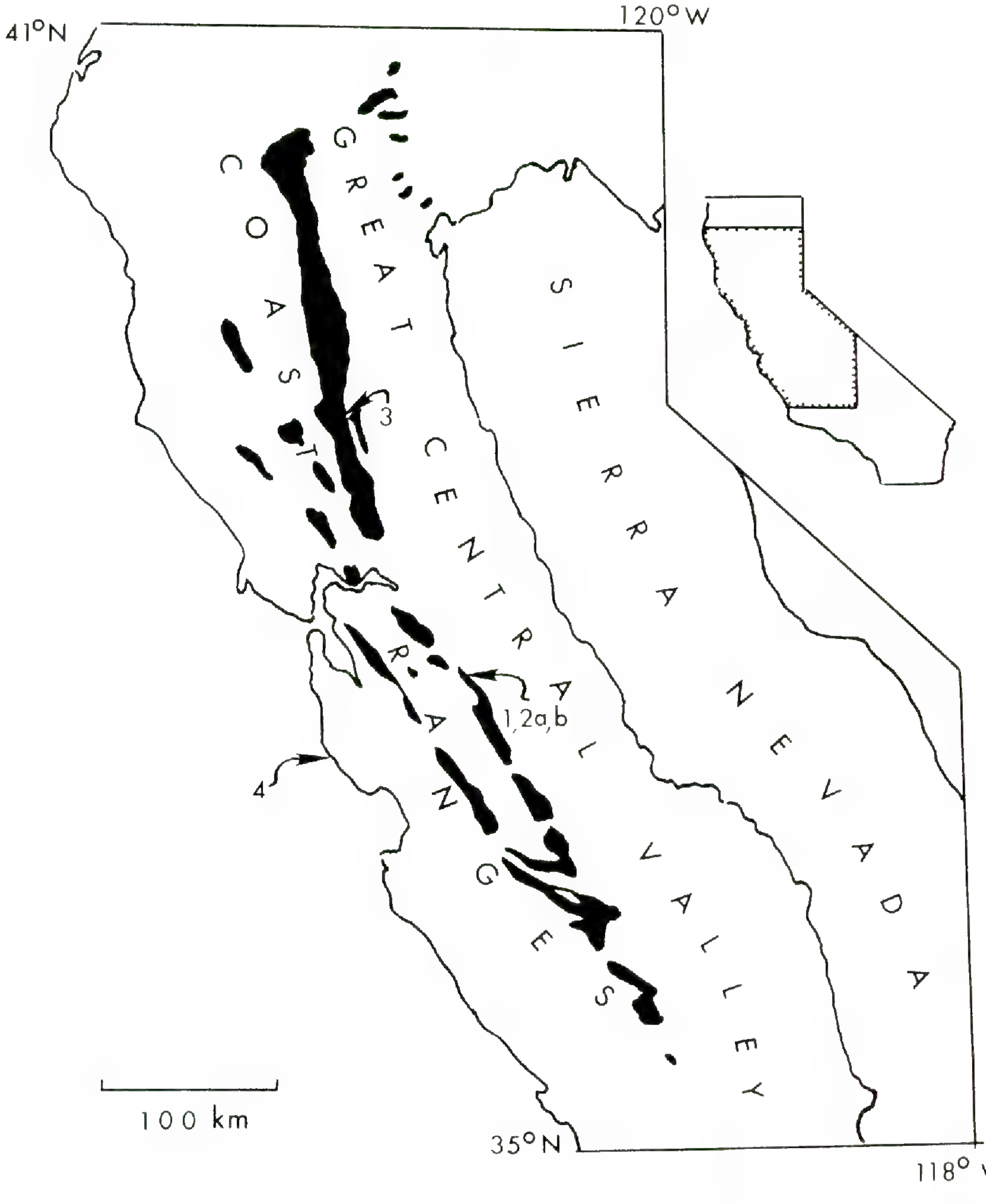

MAP 1. Great Valley Sequence of Coast Ranges (solid black), northern and central California, showing collection localities and major outcrops. Delineated area outlined in stipples in inset map of California. After Ingersoll, 1976.

from the end of the Jurassic to the beginning of the Paleocene. It is a major component of the Great Valley Sequence, which crops out mainly along the eastern flank of the inner coast ranges bordering the Great Central Valley. The southern portion of this valley is known as the San Joaquin Valley, and the northern portion as the Sacramento Valley. Most of the Great Valley Sequence outcrops that have been investigated are turbidites, and the sediments were probably deposited as subsea fans built into a deep trough, which by Maastrichtian time was nearly filled (Dickinson & Rich, 1972). The source

of the sediments was a magmatic arc that occupied the western continental margin of Mesozoic North America (Hamilton, 1969). Final deposition of the wood specimens collected from localities 1, 2a, and 2b was probably on the slope of the continental shelf (Ingersoll, 1976). Ingersoll (1979) calculated the average sedimentation rates for each fan facies association and for each stage of the Great Valley Sequence; he found that the rate for shelf-slope deposits during the Maastrichtian was about 250 meters per million years. On the basis of these calculations, the distance of 365 meters between localities 1 and 2a shown in Chmura's columnar sections represents an interval of almost 1.5 million years. As will be pointed out later, this time interval could account for some of the differences observed between the fossil assemblages derived from locality 1 and those from 2a and 2b.

The nature of the depositional environment presupposes river systems draining into the sea, possibly with the formation of extensive deltas. The Late Cretaceous paleogeographic history of California is complex and is not completely understood. It is currently held that the magmatic arc in northern and central California migrated eastward concomitant with an easterly transgression of the sea (Ingersoll, 1979), and that these events were controlled by a subduction complex to the west of the continental margin (Hamilton, 1969). Tectonic activity and sea level changes could have had profound effects on the vegetation, particularly on occupants of tidal zones and nearshore habitats.

SYSTEMATICS

Of the nearly 200 specimens of dicotyledonous wood collected from the four localities, only half proved to be sufficiently well preserved to be useful in the present study; of this half, 60 have been described (Page, 1967, 1968, 1970, 1979, 1980). It was impossible in most instances to determine the modern affinities of these specimens (Page, 1979). In general, efforts to establish modern correlatives of pre-Tertiary dicotyledonous woods are frustrated by such obstacles as poor preservation, which obscures critical anatomic features; the existence of closely similar wood patterns in unrelated families; and the great amount of time that has elapsed since the close of the Cretaceous, during which significant evolutionary changes can be expected to have taken place. The assemblage discussed here presented additional problems inasmuch as at least 70 percent of the specimens represent small stems, branches, or roots. It is unfortunate that most descriptions of modern woods are based on mature secondary xylem: in many species significant anatomic changes occur during the early stages of growth in the stem, and equally significant differences may exist between stems and roots of the same plant. After a series of unrewarding efforts to establish affinities of these fossils, it appeared that the only way to deal with them was exclusively on the basis of structural patterns, without reference to specific modern genera or families. To arrange the fossils in some kind of order, which would facilitate comparisons among the specimens and also with other woods, an artificial system of classification was constructed. This scheme is based on wood characters that are most

likely both to be preserved in fossil material and to be mentioned in descriptions of modern woods. The classification is presented in full by Page (1979), with suggested revisions by Page (1980).

Although most specimens are distinctly different from one another, duplicates of some structural patterns were observed. In addition, there are a few groups of specimens that are similar in many respects but different in others. These differences are interpreted as being of the kind often observed between species of a genus, among individuals of a species, or between roots and stems of the same plant, and thus are not considered sufficient to warrant delineation of distinct patterns within the groups. When all the duplicates are taken into consideration, the total number of distinct structural patterns appears to be 47.

Specimens representing the 47 basic patterns are listed below according to their position in the proposed classification and are identified by their accession number. Numbers preceded by CASG represent specimens deposited in the California Academy of Sciences geologic collections in San Francisco, while those preceded by SUPTC are deposited in the Stanford University Paleontology Type Collections now housed at the California Academy of Sciences. To provide a frame of reference within which to view the fossil assemblage, examples of modern families with genera having wood patterns similar to particular fossil patterns are included in the list. Because the groupings in the classification are based on gross structural features, inclusion of a variety of wood patterns within a grouping is to be expected; therefore, more than one fossil pattern as well as more than one genus in more than one family may be included within a subgroup. In addition, the broad range of variation in wood structure characteristic of some families may result in the inclusion of more than one basic pattern within a family, and as pointed out above, closely similar patterns may occur in related or unrelated families. For example, the patterns classified as Group IIB occur in at least six families, and the structural pattern exemplified by specimen CASG 60119 can be observed in species of *Clethra* (Clethraceae), as well as in some members of the Nyssaceae and Theaceae. CASG 60118 represents a pattern that also occurs in that portion of the ranges of variation within the woods of the Nyssaceae and Theaceae that overlaps with the Icacinaceae (exemplified by *Platea*) and the Aquifoliaceae (exemplified by *Phelline*). In three instances, modern analogues of the fossil patterns were not found. Localities from which all specimens of a given fossil pattern were collected are included in the list. It must be emphasized that the list of families and genera is not a list of identifications. Similarities of structure between fossils and modern taxa do not necessarily imply phylogenetic relationship.

A CLASSIFICATION OF UPPER CRETACEOUS DICOTYLEDONOUS WOODS FROM CENTRAL CALIFORNIA AND EXAMPLES OF THEIR MODERN ANALOGUES

GROUP I. Vessels absent:

CASG 60116—locality 1; Old World Winteraceae.

SUPTC 6855—locality 1; Tetracentraceae.

GROUP II. Pores mostly solitary, perforations scalariform, bars averaging more than 50:

A. Axial parenchyma absent:

CASG 60120—locality 2b; Illiciaceae, Monimiaceae (*Matthaea*).

SUPTC 10001—locality 2a; Eupomatiaceae, Chloranthaceae.

B. Axial parenchyma apotracheal:

CASG 60119—localities 1, 2a; Clethraceae, Nyssaceae, Theaceae.

CASG 60130—locality 2a; Dilleniaceae (Dillenioideae).

CASG 60118—locality 2a; Nyssaceae, Theaceae, Icacinaceae (*Platea*), Aquifoliaceae (*Phelline*).

GROUP III. Pores mostly solitary, perforations scalariform, bars averaging fewer than 50:

B2. Axial parenchyma mostly apotracheal, vessel pits opposite-transitional:

CASG 60122, 60125, 60127, 60128—localities 1, 2a, 2b; Theaceae, Symplocaceae, Cornaceae, Euphorbiaceae (*Protomegabaria*).

CASG 60129—locality 1; Cornaceae (*Cornus*), Theaceae (*Laplacea*), Cunoniaceae (*Weinmannia*).

CASG 60131—locality 2a; Cunoniaceae, Eucryphiaceae.

CASG 60132—locality 1; Icacinaceae.

SUPTC 9938—localities 1, 2a, 2b; Platanaceae.

SUPTC 9939—locality 2a; Icacinaceae (*Citronella*).

CASG 60134—locality 2a; Hamamelidaceae.

B3. Axial parenchyma mostly apotracheal, vessel pits opposite and alternate:

SUPTC 10000—localities 1, 2a, 2b; Escalloniaceae, Epacridaceae, Grossulariaceae.

CASG 60206—locality 1; Cornaceae, Ericaceae, Icacinaceae (*Apodytes*).

CASG 60135—locality 2b; Ericaceae.

CASG 60207—locality 2a; Cornaceae, Icacinaceae, Caprifoliaceae.

CASG 60133—locality 1; Myricaceae, Ericaceae, Escalloniaceae, Cunoniaceae.

C. Paratracheal parenchyma present:

CASG 60420—locality 3; Araliaceae, Dilleniaceae.

CASG 60421—locality 1; Dilleniaceae, Cunoniaceae (*Kaunbachia*).

CASG 60422—locality 1.

GROUP V. Pores in multiples as well as solitary, perforations scalariform, bars averaging fewer than 50:

A. Axial parenchyma absent:

CASG 60423—locality 2a; Araliaceae, Rhizophoraceae.

CASG 60424—localities 1, 2a; Lacistemaceae, Flacourtiaceae, Violaceae.

B. Axial parenchyma apotracheal:

CASG 60425—localities 1, 2a; Magnoliaceae.

CASG 60426—locality 2a; Aquifoliaceae (*Ilex*), Olacaceae (*Strombosia*), Clethraceae.

GROUP VIB. Perforations simple and scalariform, pores mostly solitary, axial parenchyma apotracheal:

CASG 60428—locality 2a; Juglandaceae (*Engelhardtia*), Fagaceae.

GROUP VII. Perforations simple and scalariform, pores in multiples as well as solitary:

B. Axial parenchyma apotracheal:

SUPTC 99999—locality 2a; Betulaceae (Coryleae).

C. Paratracheal parenchyma present:

CASG 60427—locality 1; Araliaceae, Leeaceae.

GROUP VIII. Perforations simple, intervessel pits scalariform, transitional, or opposite:

A. Axial parenchyma absent:

CASG 60429—locality 2a; Araliaceae, Fagaceae (*Nothofagus*).

B. Axial parenchyma apotracheal:

CASG 60430—locality 2b; Cunoniaceae, Fagaceae (*Nothofagus*), Olacaceae.

GROUP IX. Perforations simple, intervessel pits alternate, axial parenchyma absent:

CASG 60432—locality 1; Compositae, Solanaceae.

CASG 60433—locality 1; Euphorbiaceae, Moraceae, Rubiaceae, Sonneratiaceae.

GROUP XA. Perforations simple, intervessel pits alternate, axial parenchyma apotracheal-diffuse:

CASG 60434—locality 1.

CASG 60435—locality 1; Betulaceae (Coryleae).

CASG 60419—localities 2a, 4; Myrtaceae, Rosaceae (*Licania, Parinaria*).

GROUP XIA. Perforations simple, intervessel pits alternate, axial parenchyma vasicentric:

SUPTC 6867, CASG 60439, CASG 60440—localities 1, 2a, 2b; Lauraceae.

CASG 60443, CASG 60445—localities 1, 2a, 2b; Sapindales.

CASG 60447—locality 1; Combretaceae, Leguminosae.

CASG 60448—locality 2b.

SUPTC 99998—locality 2a; Menispermaceae (*Cocculus*), Lardizabalaceae.

Although similarities between the fossil specimens and their modern approximations are not regarded as indicating affinity, there are a few instances in which circumstances (such as similarities in accessory tissues or the presence of special kinds of cells) may warrant reference to a particular modern genus or family. For example, the platanoid fossil, SUPTC 9938, is similar in every way to the wood of the modern genus *Platanus* except for the absence of simple perforations in the fossil (Page, 1968). Even the bark and pith regions are similar. Some of the lauracioid fossils are closely similar to woods of certain genera of the Lauraceae. In some of these fossils enlarged parenchyma cells, like the secretory cells in members of that family, are present; in others, ray or axial parenchyma cells may contain an amber-colored substance resembling the contents of secretory cells but differ little in either size or shape from other parenchyma cells. Nests of sclereids, which are not uncommon in the pith of some members of the Lauraceae, are also present in those fossils that have enlarged parenchyma cells (Page, 1980).

Phosphatic nodules associated with the fossil woods from localities 1 and 2a contain a rich assortment of angiosperm and gymnosperm pollen, as well as other palynomorphs. The dicotyledonous pollen has been described by Chmura (1973). Some of the modern taxa she has identified in the pollen assemblage also have counterparts among the wood fossils. The most common pollen species in localities 1 and 2a is *Cupaneidites carlquistii* (Drugg) Chmura; four additional species of the genus are present but are not as abundant. According to Chmura, all have affinities with the tribe Cupanieae of the Sapindaceae. One of the most common wood patterns in localities 1, 2a, and 2b has close counterparts in the Sapindales. In comparison with the range of wood characteristics exhibited within the order Sapindales at the present time, the sapindalioid fossil woods described here are relatively unspecialized, but such patterns are to be found in certain genera of a number of families in the order, including the Sapindaceae. Another common pollen form is *Triporopollenites scabroporus* Newman, which Chmura considers close to the pollen of *Symplocos*. Although the wood of *Symplocos* is very similar to one of the most common patterns in the fossil assemblage, there are genera in several other modern families with this type of wood. Seven of the 15 fossil specimens collected have been described (Page, 1979), and certain differences among them were noted. Some of these differences could be interpreted as variations that may occur among individuals of a species or between species within a genus, but others may reflect taxonomic differences of a higher order. It is possible, therefore, that more than one major taxon is represented among the 15 wood specimens, and one of them may be the family Symplocaceae or its precursor.

The Juglandaceae, Fagaceae, and Betulaceae provide other examples of families or family complexes that may occur in both the pollen and the wood assemblages. A common pollen species in localities 1 and 2a is *Myricipites cavilleratus* (Drugg) Chmura, which has close similarities to the pollen of both *Engelhardtia* and *Alfaroa* of the Juglandaceae. The wood specimen (CASG 60428), which has structural counterparts in both the Juglandaceae and the Fagaceae, cannot be identified with any one genus of either family (Page, 1980); it is, however, closest to *Engelhardtia* except for the presence of vascular tracheids in the fossil. Tracheids are characteristic of many members of the Fagaceae, but only of *Platycarya* in the Juglandaceae. Pollen attributable to the Fagaceae (*Castanea*) is also reported by Chmura. Another common pollen species, *Plicopollis thornei* (Drugg) Chmura, is similar to the pollen of the Betulaceae and of the Rhoipteleaceae. Three of the fossil woods described (SUPTC 99999, CASG 60435, and CASG 60436) have similar counterparts in the Coryleae of the Betulaceae (Page, 1970, 1980) but, again, cannot be identified closely with any one genus. It is significant that in none of the above instances can either the pollen or the wood be assigned to a particular family with any degree of certainty. The three families involved are considered by most systematists to be related, and they are grouped together within the subclass Hamamelidae by both Cronquist (1968) and Takhtajan (1969). It is within reason to suggest that these families were not as clearly delimited in the Late Cretaceous as they are now and that the fossils represent

intermediate taxa that are now extinct. Other families that have been identified (with varying degrees of certainty) among the pollen species and that also have possible counterparts in the fossil wood assemblage are the Illiciaceae, Eupomatiaceae, Chloranthaceae, Aquifoliaceae (*Ilex*), Solanaceae, Myricaceae, Menispermaceae, Hamamelidaceae, and Nyssaceae.

FLORISTICS

Chmura (1973) recorded a total of 75 distinct angiosperm pollen species from localities 1 (her locality 5) and 2a (her locality 4). The wood assemblage does not display as much diversity, possibly because it represents plants within a limited habitat range; the number of specimens collected is also far smaller. My own examination of some of Chmura's preparations from the two localities (Page, unpubl.) indicates that gymnosperms—particularly conifers—were an important element of the vegetation. Species of Araucariaceae, Taxodiaceae-Cupressaceae, Podocarpaceae (*Phyllocladites*), and Pinaceae, several slightly rugulate forms that may be either Podocarpaceae or Pinaceae, and the pollen genera *Classopollis* and *Caytoniapollenites* were recognized. There are also monosulcate forms as well as numerous fern spores, the most conspicuous of which are *Cicatricosisporites*, *Gleicheniidites*, and large grains of *Cyathiodites*. Although the pollen and spore assemblage indicates a substantial and diverse gymnosperm element as well as the presence of a variety of ferns, there is no evidence of ferns and little indication of gymnosperms among the megafossils. Only one specimen of gymnosperm wood (CASG 60826) was collected from locality 2b and none from 2a, while seven were collected from locality 1. One type of gymnosperm wood from locality 1 has been described as an extinct member of the Taxodiaceae (Page, 1973). Another, CASG 60450, has both vertical and horizontal resin canals and is probably related to the Pinaceae. A third, CASG 60451, is a small branch with scalelike leaves and *Cupressinoxylon* wood. The remainder, CASG 60121, 60123, 60823, and 60824, have no distinguishing characteristics but differ from one another in tracheid size and amount of axial parenchyma.

Of the 75 pollen species described by Chmura, 47 were found in nodules from locality 1 and 69 from locality 2a. Twenty-eight of the species from 2a were not observed in locality 1, and seven of those from locality 1 were not observed in nodules from 2a. The gymnosperm and fern components appeared to be the same in the two localities, but substantiation of this impression requires more study. The differences between the wood assemblages from these localities are not as striking as those of the angiosperm pollen. The most obvious are the occurrence of the two vesselless forms as well as the most advanced (Compositae-Solanaceae) only in locality 1, and forms resembling the woods of *Eupomatia*, *Cocculus*, and *Licania* only in 2a. These sorts of differences, in addition to those in pollen composition and the total lack of gymnosperm wood in 2a, may reflect a real dissimilarity, if not in composition of the vegetation, at least in distribution of individual species. In the more than a million-year time interval between 1 and 2a, there may have been climatic as well as extensive topographical changes that could have altered distributional patterns among the plants—hence their distance from the basin of deposition.

Lack of growth rings in all but 19 of the 71 wood specimens with sufficient cross-sectional area exhibiting a good state of preservation suggests that the climate during the time span from localities 2b through 1 was probably equable, possibly with wet and dry seasonal fluctuations. Only one specimen (CASG 60427) shows what could be interpreted as a semi–ring porous condition, but even this is questionable because the condition can be observed in only a small portion of the transverse section and cannot be traced laterally due to the poor state of preservation. Growth rings, when present, are generally faint and can be detected only with magnification. Of the few specimens of mature secondary xylem, detectable rings were observed in only one (CASG 60439), and there was no difference among the localities in the total number of specimens with growth rings. Among the conifer woods, the single specimen (CASG 60826) from locality 2b has wide rings; of those from locality 1, CASG 60450, the probable Pinaceae, has definite rings, while the remainder have indistinct ones or none at all. Further evidence of equable climatic conditions is provided by the fact that the majority of angiosperm wood patterns found among the fossils occur today in plants of warm latitudes. The presence of woody monocots (as indicated by a small fragment of stem or frond rachis from locality 2b (CASG 60825)) and pollen attributable to *Agave* (*Liliacidites pallucibilis* Chmura) and possible palms (*Palmaeopollenites* sp. from localities 1 and 2a and *?Proxapertites* sp. from locality 2a) are indications of subtropical or tropical conditions.

EVOLUTIONARY SIGNIFICANCE

As the classification of the fossil specimens indicates, there is a high proportion of forms with characters that are generally considered to be primitive (Groups I–V), and there are none with highly specialized features such as banded, aliform, or confluent axial parenchyma (Groups XB and XIB). What is not apparent from the list is the absence of storied structure, included phloem, resin canals, gum ducts, or rays composed of tile cells—features that are considered to be highly specialized among modern plants. Since these structural features have not yet been observed in any pre-Tertiary woods of confirmed provenance,[1] it is tempting to suggest that such specializations had not yet evolved (Wolfe *et al.*, 1975). If this is the case, it is of interest to assess the present fossil assemblage relative to the range of characteristics known to exist among modern woods.

[1]The "Aptian" wood specimen described by Stopes (1912) as similar in structure to the woods of Dipterocarpaceae is not included in the above discussion because I am not convinced that the specimen has the features diagnostic of that family, or that the age assignment is reliable. I had an opportunity to study the slide preparations in the British Museum (Natural History) and found the preservations poor; although there appeared to be parenchymatous patches in transverse section and holes resembling vertical ducts, neither feature could be verified in longitudinal section. Other kinds of specialization were evident, however, such as vasicentric tracheids and vessel elements of short to medium length (364–728 μm.). The provenance of the specimens is far from certain. The post-Jurassic geologic history of England is complex (Kellaway *et al.*, 1971), for erosion and resedimentation had occurred all through the Cretaceous

Before comparisons between the fossil assemblage and modern woods are made, two problems must be resolved. First, 70 percent of the specimens are small stems between 2.5 cm. and 5 cm. in diameter. It is well known that early-formed secondary xylem of stems may differ in many ways from that of mature wood, but most descriptions and available reference material are only of mature wood. Second, very little is known about the relationship between anatomic structure of stems and habitat preference. It is important to know whether habitat bias may account for the lack of highly specialized anatomic structures and the high proportion of primitive structures. As to the first question, a preliminary survey of young stems of plants with various types of specialized tissues indicated that specializations tend to appear within the first half-centimeter increment of secondary xylem: for example, storied elements in *Asimina, Isomeris, Larrea, Artemisia, Sterculia;* included phloem in *Forchhammeria* and *Avicennia;* banded parenchyma in *Trophis* and many Leguminosae; and tile cells in *Sterculia.* Perhaps there are some species in which development of specialized patterns typical of the mature wood is delayed beyond the first half-centimeter of increment, but establishment of this possibility must await a more thorough survey. In any case, most stems in the fossil assemblage consist of a radius of 0.5 cm. or more of secondary xylem; therefore, the probabilities are fairly high that the lack of the above-mentioned specializations is not due to the low representation of developmentally mature wood. Vertical and horizontal canals and complex pore arrangements were not included in the survey because there is some variation among species in the time during ontogeny of the stem when these features are established. Furthermore, canals may occur sporadically in the woods of some species so that several sections may be needed to establish their presence. For these reasons, the absence of resin canals and complex pore arrangements may or may not be significant.

As to the second question, most of the plants from which the fossils were derived probably grew along watercourses close to the sea or in any of

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and Tertiary. Moreover, during the Pleistocene, an enormously thick layer of glacial drift covered much of the southern part of the country. Most of the drift has eroded away, but isolated pockets remain. These pockets contain a large number of erratics—many known to have been carried from as far away as Norway. Such erratics can be found in scattered places other than drift pockets. The "Aptian" woods described by Stopes (1912, 1915) may have been such erratics fortuitously deposited in the vicinity of the fossiliferous exposures purported to have yielded these specimens. A person happening upon such a fossil would naturally assume that it had been derived from the nearby fossiliferous outcrops, which in these cases were known to have contained wood. It is significant that, despite repeated efforts, no other angiosperm wood has ever been recovered from any of the four localities from which these "Aptian" woods were supposed to have been collected (Hughes, 1961). It is also significant that Stopes, herself, was not entirely sure of the reliability of the labels accompanying the specimens, all of which had been transferred to the British Museum from other repositories. The Cretaceous age assignment of a specimen from Somaliland described by Chiarugi (1929) as having aliform parenchyma is also poorly documented. A highly specialized wood from Japan described as a species of *Chionanthus* (Suzuki & Nishida, 1974) was found as a float on a beach in the vicinity of an Upper Cretaceous outcrop, from which it was assumed to have been derived.

a variety of coastal habitats. To discover whether certain specializations in wood tissue are more or less likely to be found in plants growing in such environments, floristic studies of several regions throughout the world were examined to determine habitats of species for which anatomic information was available. Information was obtained for 364 species. For practical reasons, the survey was limited to determining the arrangement of axial parenchyma and the presence or absence of storied elements. The frequency of these characters was determined for riparian, coastal, and inland or upland species. The results are presented in TABLE 1. The frequency of storied structure among 1800 species surveyed by Metcalfe and Chalk (1950) is included for comparison. Unfortunately, similar data were not available for the frequency of the different types of axial parenchyma patterns. The discrepancy between my data and those of Metcalfe and Chalk is very likely due to the high proportion of unspecialized woods in my reference collections. Although not necessarily restricted to these habitats, of the 364 species surveyed, 88 representing 44 genera occur in riparian habitats, 102 representing 49 genera occupy coastal areas, and 235 representing 86 genera are in inland or upland habitats.

The figures in TABLE 1 indicate that storied elements and complex parenchyma patterns are to be found in a significant number of coastal and riparian species. It must be emphasized that in most of the floras consulted, habitat specifications were not precise; thus, the data presented are equally inexact. The data suggest, however, a correlation between ecological factors and the frequency of species with storied and/or particular patterns of axial parenchyma; therefore, a more thorough investigation might be worthwhile. In any case, rather than indicating a bias against plants with these particular features, the figures show the occurrence of the features in a significantly higher percentage of coastal and riparian species. When the dicots are considered as a whole, a more careful and detailed investigation may reveal a definite correlation between specializations in wood anatomy and particular habitats (see Carlquist, 1975). Deltaic and fluvial deposits may be just where the earliest evidence of structural innovations in secondary xylem will be found.

Extensive investigations earlier in this century (Bailey & Tupper, 1918;

TABLE 1. **Percentage of species in modern flora with storied elements or advanced parenchyma patterns.**

	STORIED ELEMENTS	BANDED AND/OR ALIFORM-CONFLUENT PARENCHYMA
Modern flora (M & C)	14	
Modern flora (VP)	10	22
Inland spp.	6	25
Coastal spp.	13	40
Riparian spp.	16	29

Explanation of abbreviations: M & C, from Metcalfe and Chalk, 1950; VP, from author's references.

Barghoorn, 1940, 1941a, 1941b; Frost, 1930a, 1930b, 1931; Kribs, 1935, 1937) have provided us with a well-documented basis for hypotheses outlining the phylogenetic progression of the various structural components of the secondary xylem in dicotyledons as a whole. A brief summary is presented here, and a more detailed one is included in Carlquist (1961). Phylogenetic modifications in conducting cells resulted in progression from long tracheids to the formation of long elements with multiple perforations. Further modifications resulted in the reduction in length of the vessel elements and in reduction in the number of perforations from many on an acutely slanting end wall to a single horizontal opening. Wall pitting progressed from scalariform to opposite to alternate. Trends in axial parenchyma were from diffuse-apotracheal to a variety of patterns, some of the most specialized of which are wide tangential bands that may or may not engulf vessels or groups of vessels. Primitive rays are high and heterocellular. Uniseriate margins of the multicellular rays consist of many layers of square or upright cells. The chief trends in phylogenetic modifications are interpreted as being toward elimination of either multiseriate or uniseriate rays or both, a decrease in height, and reduction or elimination of uniseriate margins. Cellular components became less heterogeneous until both multiseriate and uniseriate rays were composed only of procumbent cells. Tile cells, found in the wood of certain genera of the Malvales, are a special kind of modification. In a limited number of taxa, a further kind of specialization occurs in the cambial initials, which become tangentially aligned in vertical rows. Minimal subsequent elongation of daughter cells during maturation may result in the storying of such tissues as parenchyma, rays, or vessel elements. Since these suggested trends appear plausible as seen from the perspective of the modern flora, it would be of interest to discover whether they seem so from the perspective of earlier periods. Unfortunately, the currently available information about Cretaceous woods is inadequate for such an evaluation.

If we assume that the proposed sequences of evolutionary modifications reflect what actually took place, it is possible to arrive at some indication of the level of specialization attained in the secondary xylem of dicotyledons at a given time in the past by comparing frequencies of the various types of structural modifications in modern and fossil woods. The least specialized fossil patterns in the assemblage under discussion are the vesselless forms, while the most highly specialized is specimen CASG 60432, which is similar to the wood of some Compositae. Between these two extremes there is a variety of specializations in ray and vessel structure and in axial parenchyma distribution. In a few specimens the rays consist almost entirely of procumbent cells, in others uniseriate rays are scarce, and in several only uniseriates could be observed. In the majority the rays are heterocellular, both multiseriates and uniseriates are present, and the multiseriates have uniseriate margins. Among specimens with axial parenchyma, the fossils were evenly divided between those with only apotracheal and those in which paratracheal parenchyma is present. A survey of modern woods revealed that there is no significant difference in the frequency of the two types of parenchyma distribution. Axial parenchyma is absent or sparse in several specimens.

Apotracheal parenchyma is diffuse in most but occurs in short uniseriate tangential lines in some. Paratracheal parenchyma consists mostly of a few cells associated with the vessels, but in two patterns it forms sheaths one or two cells thick, and in one the sheaths are as many as three cells thick.

Aside from the absence of advanced parenchyma patterns, storied elements, included phloem, tile cells, resin ducts, and complex pore arrangements, the most striking characteristic of the fossil assemblage is the high incidence of primitive features in the vascular tissue. The degree of evolutionary advancement in this tissue in the perforate forms is best shown in the length of vessel elements and in the nature of the end wall perforations. In order to make comparisons with the modern flora, the frequency of simple, scalariform, and simple and scalariform perforations—as well as that of each of three categories of average element length—were calculated. The results are presented in TABLE 2 together with similar information for modern woods based on data obtained from Metcalfe and Chalk (1950). The percentage of the various types of perforation plates in inland, riparian, and coastal species were obtained from 339 genera in my reference collection. Data on vessel element length for these species were not included because of inadequate information. Such data may not be necessary at this time for, as Frost (1930a) discovered, there is a positive correlation between evolutionary advancement in the end walls of vessel segments and the length of those segments; thus, a low percentage of scalariform perforations in the modern flora is indicative of a generally low incidence of long vessel elements. Because of the necessarily subjective method used for determining basic anatomic patterns and the possible introduction of bias in favor of one or another grouping in this analysis, figures were compiled for the assemblage of specimens as a whole as well as for the basic patterns listed earlier. Any judgmental bias would be most significant in evaluating the status of the lauracioid (14 specimens),

TABLE 2. **Percentage of perforation plate types and average vessel element lengths in modern flora and fossil assemblage.**

	PERFORATION PLATE TYPE			AVERAGE VESSEL ELEMENT LENGTH (mm.)		
	SC	S	SS	.8	.4–.8	.4
Fossils						
Basic patterns	60	33	6	26.6	62	11
Assemblage	57	40	3	26.6	65	8
Modern flora (M & C)	11	83	5	25.0	44	31
Modern flora (VP)	20	73	6			
Inland species	31	63	6			
Coastal species	17	82	1			
Riparian species	16	77	6			

Explanation of abbreviations: M & C, from Metcalfe and Chalk, 1950; VP, from author's references; SC, scalariform; S, simple; SS, simple and scalariform.

the sapindalioid (11 specimens), and the symplocacioid (15 specimens) groups, for among them there are 15 with scalariform and 25 with simple perforations. All other basic patterns are represented by from one to three specimens. Figures for type of end wall were based on 95 specimens, and vessel element length on 75. The data in TABLE 2 show that no matter which fossil group is used for comparison, the modern flora contains a far lower proportion of forms with scalariform perforations and a correspondingly higher proportion with short (less than .4 mm.) vessel elements. The figures also show that there is a lower proportion of species with scalariform perforations in coastal and riparian than in upland habitats. Carlquist (1975) has suggested that because of constraints placed upon the efficiency of conducting systems composed of tracheids or vessels with scalariform perforations, plants with such systems are confined to mesic habitats, where water loss through transpiration is not excessive and low rates of water conduction are not disadvantageous. Evidence that tends to support this hypothesis has been presented by Baas (1976). According to both of these authors, the high representation in mesic habitats of forms with simple perforations is a result of secondary adaptive invasion since simple perforations presumably evolved under xeric environmental conditions. If simple perforations render a conducting system more efficient under conditions of high transpiration, then it seems plausible that forms with this more efficient system would have the potential for greater adaptability to a variety of conditions given the possibility of control of water loss through evolutionary modification of leaf, root, and/or bark structure. Adaptive potential of forms with only tracheids or vessels with exclusively scalariform perforations, on the other hand, would be dictated by the limitations of their conducting systems. However this may be, the percentage of patterns with scalariform perforations only is far higher in the fossil assemblage than in any modern mesic flora or florula listed by Baas (1976), who conducted a survey of such genera from a large number of floras representing a variety of environmental conditions. Several explanations of this phenomenon come to mind. For example, there may be no environmental regime today comparable to that which prevailed in the region occupied by the source plants of the fossils. Alternatively, species with simple perforations may have become established in only a few lineages and would therefore have been low in numbers. Or there may have been fewer species with simple perforations in this region than in other parts of the world. Or, perhaps few species with simple perforations became adapted to riparian or coastal habitats. As I shall discuss later, however, at least some species with simple perforations were established in such environments as early as the Aptian–Albian and are among the earliest-known examples of dicotyledonous wood in the fossil record.

On the basis of ray structure and parenchyma distribution, the fossil assemblage represents what may be considered a moderate level of advancement in comparison with the range of characteristics present in the modern flora. The high proportion of vessels of medium length (0.4–0.8 mm.) is consistent with that evaluation, but the fact that the percentage of scalariform perforations in the fossils is over four times that in the modern flora is indicative of

a lower level of advancement. There is a possibility that the measurements of vessel elements in the fossils are generally low and may not reflect the condition of the mature wood of the parent plants, for elements formed early in the ontogeny of the stem tend to be shorter than those formed in later increments (Bailey & Tupper, 1918). In addition, measurements in the fossils must, of necessity, be made from sectioned material; hence, it is usually not possible to measure the entire element but only the distance between perforation plates of an element. Measurements in modern woods, on the other hand, are usually of macerated tissues; therefore, the length of the whole segment is obtained. A higher incidence of long vessel elements would be more consistent with the high frequency of scalariform perforation plates in the fossil assemblage.

Whether the level of advancement of the small collection of fossil woods reported on here reflects the condition prevailing universally at the close of the Cretaceous cannot be judged at the present time because of a paucity of information about Cretaceous dicot woods in general—including data for this assemblage, fewer than 100 species have been reported from the entire period. The lack of reliable age assignments for many of the fossils described has presented a problem in compiling data about most Cretaceous and many early Tertiary woods. In addition, descriptions, particularly in the older literature, often lack important information, and illustrations consist only of drawings (if photomicrographs are included, they are of poor quality and only of transverse sections). According to information available at the present time, there is no reliable record of complex parenchyma patterns, storied elements, included phloem, resin canals, gum ducts, complex vessel distribution, or tile cells in pre-Tertiary woods. The earliest-known banded parenchyma occurring in wood from a well-documented source dates from the Paleocene of Africa (Koeniguer, 1969, 1971). One species is illustrated only by drawings of transverse sections; a second clearly shows tangential bands in photographs of transverse sections, but there is no evidence that they consist of parenchyma cells, for longitudinal sections were not included and the preservation was generally poor. Horizontal canals have been described from the Lower Eocene of England (Brett, 1966), and Manchester (1979, 1980) has reported the earliest-known occurrence of tile cells—from the Middle Eocene of Oregon. An assemblage from the late Lower Eocene fluvial deposits of Eden Valley, Wyoming (Kruse, 1954), provides an interesting contrast to the California Cretaceous assemblage. Both were probably derived from streamside or near-stream habitats, and both consist of young stems, branches, or roots. However, the Eden Valley woods are generally far more highly specialized and among them exhibit the earliest evidence of storied elements, interxylary phloem, and very short vessel elements; banded parenchyma and radial canals are also present. It is clear that at least by Eocene time features that are considered to be highly specialized were well developed in some taxa. Manchester (1979, 1980), however, has pointed out that although tile cells and storied elements are present in the woods he has examined from the Clarno beds of Oregon, they are not as highly developed as they are in modern forms, and the fusiform initials in one species are from 30 to 60 percent longer than those

in their modern counterparts. The presence of highly specialized anatomic features in woods as old as the Lower Eocene suggests the possibility that at least some of them had evolved prior to the Tertiary. The lack of evidence of woods with such specializations prior to the Tertiary may be due to limited geographic distribution; therefore, the chances for them to be preserved would be equally limited.

Although the record of Cretaceous angiosperm woods is sparse, it may be of value to examine the information we have prior to the Maastrichtian. The earliest-known perforate woods date from the Aptian–Albian. They were collected from the Cedar Mountain Formation of Utah and described by Thayn (1973). Of the three specimens described, one is similar to the wood of *Platanus*, another to *Citronella*, and the third to *Phyllanthus*. The woods of *Citronella* and *Platanus* are structurally similar, and therefore the fossils will be designated as platanoid, while the third form will be called phyllanthoid. The platanoid forms belong to Group IIIB of my classification, while the phyllanthoid form falls into Group XIA. Rays are heterocellular in the phyllanthoid form and in one of the platanoid species but homocellular in the other platanoid form. The vessel elements are moderately long (avg. 500–700 μm.) in both basic patterns. Variations on the phyllanthoid pattern have been described in specimens from many other localities; the oldest of these specimens are from the Albian of Idaho (Spackman, 1948), the Cenomanian of Arizona (Bailey, 1924), and the Cenomanian–Santonian of Alabama (Cahoon, 1972). A specimen from the Albian of Madagascar was described by Fliche (1905) as having similarities with members of the Lauraceae. The pattern is somewhat phyllanthoid but apparently has more abundant axial parenchyma and rays with a higher proportion of procumbent cells. No secretory cells were described nor are they apparent in the illustrations. To my knowledge, the provenance and age of this specimen has not been confirmed. If it is assumed that the age assignment of these Early Cretaceous specimens is accurate, the available information indicates that at least two distinct patterns of dicotyledonous woods were in existence in the late Aptian or early Albian and that neither pattern can be considered primitive, although the platanoid forms have some primitive characteristics. The degree of advancement of these woods does not seem consistent with the low level of development observed in leaves and pollen of similar age (Doyle & Hickey, 1976). However, until we have a better record of angiosperm wood and also of pollen and leaves from these crucial sections of the Cretaceous, speculation on this point is of little value. It is of interest to note that, except for the few examples cited above and a possible imperforate angiospermous wood from Japan (Nishida, 1962), the record of dicotyledonous woods prior to the Maastrichtian is essentially blank, yet gymnosperm woods are relatively common. Obviously, there are many questions to be answered, and one can only hope that more attention will be accorded the search for and study of Cretaceous angiosperm woods in the future.

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REVISION AND EXPANSION OF THE NEOTROPICAL GENUS WERCKLEA (MALVACEAE)

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PITTIER AND STANDLEY (Standley, 1916) described the genus *Wercklea* to include a single Costa Rican species, *W. insignis*. In 1921 Rolfe added a second species, *W. lutea,* also from Costa Rica. Subsequently, *Wercklea* has been considered to be endemic to Costa Rica and to include only these two species, although it was tentatively increased to "about 2–4 species" in *Hortus Third* (Bailey Hortorium Staff, 1976). The genus has been maintained as distinct by Standley (1937), Kearney (1951), Hutchinson (1967), and Bailey Hortorium Staff (1976); Robyns (1965, 1966), however, has merged *Wercklea* in *Hibiscus* L. and has transferred the two Costa Rican species to the latter genus.

Fries (1947) recognized a "species group" that included his newly described *Hibiscus trichomathus* R. E. Fries, together with *H. hottensis* Helwig ex Urban, *H. horridus* Urban, *H. ferox* Hooker, *H. ferox* var. *metensis* Triana & Planchon, and *H. pseudoferox* Hochr.—that is to say, those species with glabrous fruits, more or less armed (prickly) herbage, and sometimes inflated calyces. He referred this group to *Hibiscus* sect. FURCARIA, following Hochreutiner (1900), but such a placement is manifestly incorrect. Moreover, it is now apparent not only that the occurrence of these distinctive prickles and the inflation of the calyces are variable within this group, but also that the presence of the prickles extends beyond the group to other similar species that lack inflated calyces and have hispid rather than glabrous fruits (*Hibiscus woodsonii* A. Robyns and *Wercklea lutea*). Thus, whether one begins with Pittier and Standley's genus *Wercklea* or with Fries's "species group" in *Hibiscus*, one converges on a larger combined group that exhibits considerable cohesiveness, both morphologically and geographically, as well as distinctness from other plants. My own observations support the opinion that *Wercklea,* as here expanded to 12 species, is generically distinct from *Hibiscus.*

Several characters other than those emphasized by Pittier and Standley support this distinctiveness. These include the often arborescent growth habit, which is found in *Hibiscus* only in the very dissimilar sect. AZANZAE DC.; the very large, long-petiolate, more or less orbicular leaves that lack foliar nectaries; the distinctive vestiture (to be discussed separately in the following paragraph); the very large and prominent stipules, of a size and conformation not otherwise found in *Hibiscus*; and the distinctive fruits, which are obovate or fusiform and often prominently beaked and winged (FIGURES 1–6). Pittier and Standley described *Wercklea* as being distinctive in having amphitropous

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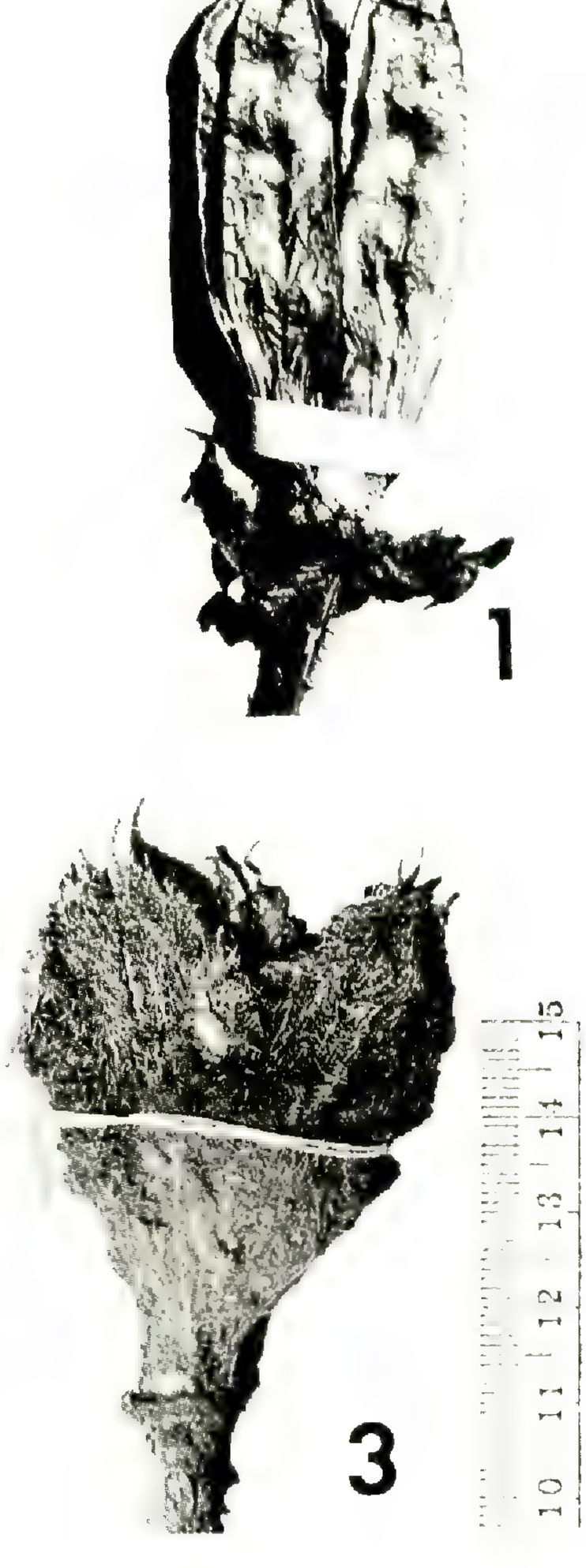
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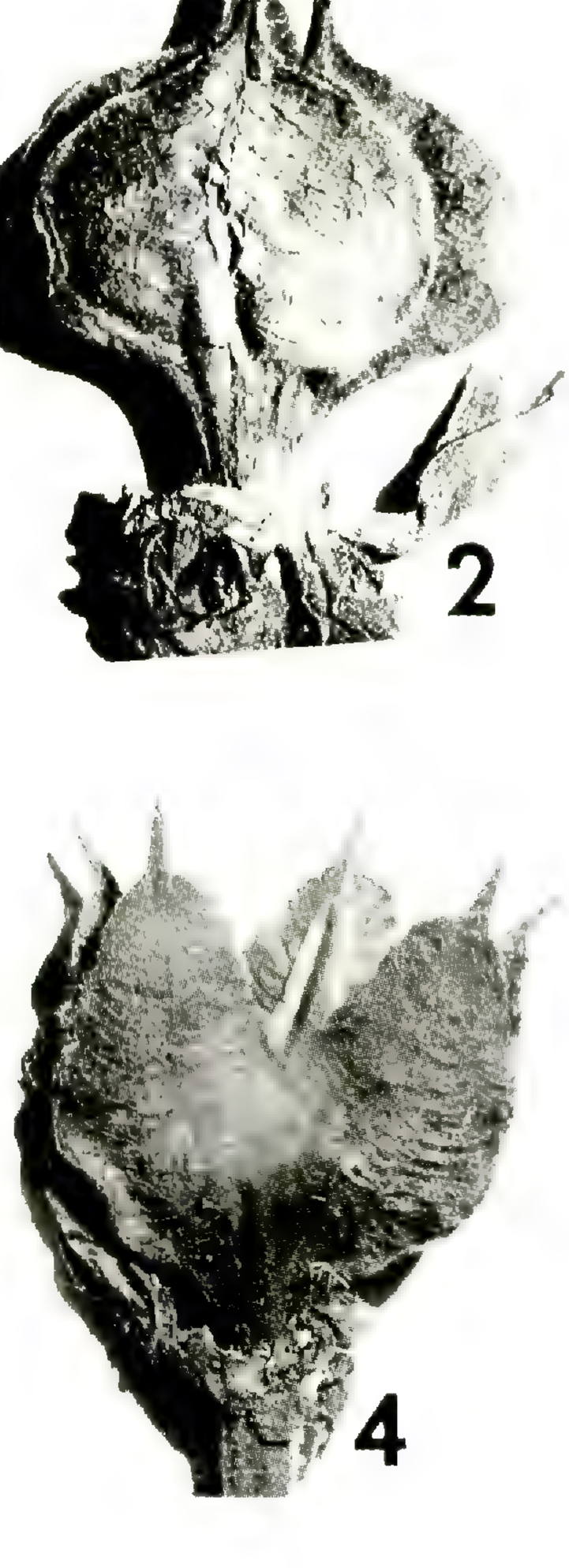
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ovules, but observations are not available to confirm the value of this character in delimiting the genus.

The vestiture of *Wercklea* is distinctive, and the following classes of hairs may be enumerated (cf. Payne, 1978): 1) stellate hairs, common throughout the family, found in all species of *Wercklea* and on nearly all plant parts, except where the plant may be glabrate (especially in *W. insignis*); 2) bristles, generally simple, often pungent; 3) pungent hairs or prickles, with a small, swollen basal cushion, usually simple but sometimes bifurcate or stellate; 4) pungent hairs or prickles with a large, yellowish, swollen column at the base and a spinescent tip; and 5) stout, conical prickles, themselves often stellate-pubescent, sometimes curved, usually ligneous and yellowish, with a spinescent tip. The stellate hairs are found more or less throughout the plant in most of the species and constitute a background of vestiture upon which the other kinds of hairs are superimposed. These more specialized hairs are distributed differentially on various plant organs, depending upon the species (see TABLE 1). In species with prickly leaves, the distribution of the prickles is noteworthy: on the lower leaf surface the prickles are found on the main veins, whereas on the upper surface they occur on the lamina between the veins (FIGURES 9, 10). This pattern of distribution seems not to have been noted before, although it is distinctive of the genus as here circumscribed and appears to be unique to it.

A number of characters suggest a stronger affinity of *Wercklea* with *Abelmoschus* Medikus than with *Hibiscus*. These common characters include the frequent occurrence of pungent hairs, the relatively large leaves lacking foliar nectaries, the long-beaked fruits that are often winged (*Wercklea*) or angled (*Abelmoschus*), and other, more subtle similarities involving the form of the involucel and calyx. *Wercklea* might be regarded as a neotropical analogue of the paleotropical *Abelmoschus*. Other characters, including chromosome number, may provide a basis for evaluating this suggested relationship. Bates (pers. comm.) has found *W. ferox* to be a high polyploid, with $n = 52$ or 56 ($2n = 104$ or 112), the only chromosome number yet known for *Wercklea*. Reported chromosome numbers for *Abelmoschus* are: *A. esculentus* (L.) Moench, $2n =$ ca. 66, 72, 118, 120, 122, 130, 132; *A. ficulneus* (L.) Wight & Arnott, $2n = 72, 78$; *A. manihot* (L.) Medikus, $2n = 60, 66, 68, 130$; and *A. tuberculatus* Pal & Singh, $2n = 58$. Such variability makes it difficult to propose base numbers for these genera. The affinity of *Wercklea* and *Abelmoschus* is further suggested by the vernacular name for *W. tulipiflora* (Hooker) Fryxell ("gambo montagne" or wild okra) and by Walpers's transfer of this species to the genus *Abelmoschus*.

Several vernacular names have been recorded for species of *Wercklea*. "Pringamoza" (= nettle) has been used for both *W. ferox* (*López & Sánchez*

FIGURES 1–6. *Wercklea* fruits: 1, *W. ferox* (*Williams 819*), inflated calyx removed; 2, *W. tulipiflora* (*Duss 2323;* see FIGURE 24); 3, *W. lutea* (*Standley 38645*); 4, *W. woodsonii* (*D'Arcy 5368*); 5, *W. woodsonii* (*Nee 9999;* see FIGURE 28); 6, *W. insignis* (*Rowlee & Stork 286;* see FIGURE 20).

TABLE 1. **Distribution of specialized vestiture in Wercklea (excluding the nearly ubiquitous stellate hairs).***

SPECIES	STEMS	LEAVES	PEDICELS	INVOLUCELS	CALYCES	FRUITS
ferox	5	5	4	3	4	—
pseudoferox	5	5	4	3	4	—
magnibracteata	3	—	2	2	2	—
horrida	4	4	4	4	4	—
hottensis	4	4	4	4	4	—
flavovirens	—†	—†	—	—	—	—
lutea	5	5	3	—	3	2
woodsonii	5	—	—	—	3	2
cocleana	—	—	—	—	3	2
grandiflora	—	—	—	—	—	2?
insignis	—	—	—	—	—	2
tulipiflora	—	—	—	—	—	—

*The kinds of specialized hairs are identified by number in the text, p. 459.

†The stems and leaves of juvenile *W. flavovirens* are densely spinescent (4), but the mature plants are unarmed.

24) and *W. horrida* (*Howard & Howard 8543*), in obvious reference to the prickly character of these species. "Gambo montagne" (*Beard 235*), "gambo marron" (*Cooper 40*), and "gambo grand bois" (= wild okra) (*Duss 2323*), all used for *W. tulipiflora*, indicate a resemblance of this species to *Abelmoschus*. *Wercklia woodsonii* (A. Robyns) Fryxell (*White 41*) has been called "amapola amarilla" (= yellow poppy), descriptive of its flower. "Burío extranjero" (= foreign "burío") has been used for *W. lutea* (*Standley & Valerio 44025*), and "burío" (*Lankester & Jiménez 1348*) for *W. insignis*; both names refer to use as a source of bast fibers in making rope. The name "burío" is applied to several other species in the Malvales (*Apeiba tibourbou* Aublet, *Hampea appendiculata* (Donn. Sm.) Standley, *Heliocarpus* spp.) that have the same use (Fryxell, 1969). Such use may be general for the genus, at least for the larger (arborescent) representatives; it has been noted for *W. woodsonii* (*White 41*) and *W. tulipiflora* (*Hodge 1127*), in addition to *W. lutea* as noted above. The sap of *W. lutea* is described as mucilaginous (*Burger & Liesner 6412*), which also may be general for the genus, inasmuch as it is a character common in the family Malvaceae.

The flowers of *Wercklea ferox* (*Gentry 8801*) and *W. grandiflora* (*Nee 9842*) are described as odorless. They are "very fragrant" in *W. woodsonii* (*White 175*), and the floral odor is "slightly sweet" in *W. lutea* (*Webster et al. 12383*).

Webber (1934, quoting Hyde, 1925) described *Wercklea insignis* as having exceptionally light wood—15 lbs. per cubic foot (or a specific gravity of 0.24), comparable to that of cork.

Wercklea Pittier & Standley in Standley, Contr. U. S. Natl. Herb. **18:** 112. 1916. TYPE SPECIES: *Wercklea insignis* Pittier & Standley.

Coarse herbs, shrubs, or trees, usually 2–20 meters tall, stellate-pubescent to glabrate; stems with prominent leaf and stipule scars, sometimes with ligneous prickles on stems and spinescent prickles or pungent hairs elsewhere. Leaf blades often too large to be adequately represented on herbarium sheets (i.e., only younger leaves preserved), deeply cordate, wider than long, more or less orbicular or sometimes ovate, occasionally weakly pentagonal or 5- to 7-lobed, sharply and remotely dentate (teeth sometimes spinescent) to subentire, obtuse to acute, palmately several nerved, stellate-pubescent (especially on veins) to glabrate above and beneath, the hairs of upper surface often fewer, smaller, and with tendency toward antrorse orientation, prickles also sometimes present between veins on upper surface and on veins on lower surface; foliar nectaries absent. Petioles shorter than to longer than leaf blade, usually with pubescence like that of stem. Stipules large and prominent (FIGURES 8, 13), 1–2 times as long as broad, 5–80 mm. long, 5–45 mm. broad, sessile and amplexicaul, lanceolate to broadly ovate to semicircular, entire (rarely bifid), acute to obtuse, stellate-pubescent, caducous, leaving scars to 1.5 cm. long. Pedicels erect, one to several in leaf axils, articulate at (or near) base and thus often appearing inarticulate, shorter than subtending petiole to greatly exceeding it, sometimes accrescent in fruit, reaching 20–34 cm. or more in some species, stellate-pubescent to glabrate, sometimes also with pungent hairs or spinescent prickles, often becoming stout and ligneous in fruit. Involucel gamophyllous or of distinct bracts (or intermediate), usually shorter than calyx, deciduous or persistent, stellate-pubescent to glabrate, pungent hairs (if present) fewer than on calyx or pedicel; bracts (if distinct) 3 to 10, lanceolate, ovate, or subrhomboid. Calyx gamosepalous, deeply 5-parted or spathaceous and apically 5-toothed, stellate-pubescent and sometimes also prickly, sometimes accrescent and inflated in fruit (FIGURE 14). Corolla greenish yellow, bright yellow, orange, or rose, 6–15 cm. long, more or less stellate-pubescent (in part or throughout; stellate hairs rarely absent), campanulate or salverform. Staminal column shorter than to subequal to corolla, appearing exserted in species with salverform corollas, glabrous or stellate-pubescent, staminiferous throughout or only distally. Styles slightly exceeding androecium, connate nearly throughout (distinct only for distal few millimeters); stigmas 5, large and capitate, crowded. Fruit capsular (FIGURES 1–6), 5-loculed, oblong, obovate, or fusiform, prominently winged or unwinged, densely hispid, stellate-pubescent, or glabrous, often with prominent beak, relatively woody, dehiscent but not opening widely, internally pubescent or glabrous. Seeds about 20 per locule, reniform or phaseoloid, blackish, 2.5–4 mm. long, densely long-pubescent, short-puberulent, or glabrous.

All species appear to occur in relatively wet habitats, whether on river banks or in rain or cloud forests. Different species have different altitudinal preferences, but several of them occur at elevations relatively high for the Malvaceae (to 2700 meters for *Wercklea lutea* and *W. woodsonii*). The relatively widespread *W. ferox* occurs as low as sea level.

Many species of *Wercklea* have one or more characters that are unique or essentially so within the genus; the species can be identified on the basis of any one. Outstanding in this respect is *W. tulipiflora*, which has a

FIGURES 7–10: 7, *Wercklea flavovirens* (*Watts et al. 1548*), in flower; 8, *W. flavovirens* (*Proctor 37837*), in fruit; 9, *W. horrida* (*Ekman 14115*), leaf folded over to show differing spine pattern on upper and lower surfaces; 10, *W. ferox* (*Allen 4098*), leaf folded over to show differing spine pattern on upper and lower surfaces.

constellation of at least six such traits. Other species have no truly unique characters but may be identified on the basis of combinations thereof. These distinctive characters or character combinations are noted for each species following its description; they are, of course, also used in the construction of the key.

Standley (1937, p. 677) dedicated the genus ". . . to Carlos Wercklé, genial, tireless, and enthusiastic explorer of the Costa Rican forests, a well informed student of the flora of his adopted land."

Key to the Species of Wercklea

A. Fruits externally glabrous, sometimes enclosed by calyx; pedicels and calyx often densely beset with spinescent prickles; stems and leaves often prickly; calyx ca. 1/4- to 1/3-divided.
  B. Calyx at anthesis 2.5–6 cm. long, accrescent to 9(–13) cm. long and inflated in fruit, prominently 10-fluted; capsule internally glabrous, enclosed in spathaceous calyx. Central and South America.
    C. Pedicels usually fasciculate, shorter than subtending petiole, 2–10 cm. long at anthesis to 13 cm. long in fruit; corolla 6–9 cm. long. Costa Rica to Bolivia, usually below 1000 m. alt.. . . 1. *W. ferox.*
    C. Pedicels solitary or paired, exceeding subtending petiole, 20 cm. long at anthesis to 34 cm. long in fruit; corolla 10 cm. long or more. Colombia.
      D. Bracts of involucel 8 or 9, 20–25 mm. long, 4–6 mm. wide; leaf margins serrate, teeth spinescent. . . 2. *W. pseudoferox.*
      D. Bracts of involucel 3 to 6, 40–45 mm. long, 16–27 mm. wide; leaf margins serrate, without spines. 3. *W. magnibracteata.*
  B. Calyx at anthesis 2–3 cm. long, somewhat accrescent but neither inflated nor exceeding fruit; capsule internally pubescent, equaling or exceeding calyx. Hispaniola and Jamaica.
    E. Pedicels 11–28 cm. long, longer than subtending petiole; leaves obscurely lobed; involucel more or less gamophyllous; fruits 5 cm. long. Haiti. . . . . 5. *W. hottensis.*
    E. Pedicels up to 9 cm. long, shorter than subtending petiole; leaves manifestly lobed; involucellar bracts distinct; fruits 2–4.5 cm. long.
      F. Bracts of involucel ca. 10, lanceolate, 10–18 mm. long, less than 6 mm. wide; petals rose, pubescent internally and externally; fruits 2–3 cm. long; plant spinescent at maturity. Dominican Republic. . . . . 4. *W. horrida.*
      F. Bracts of involucel ca. 6, ovate, 25–30 mm. long, up to 12 mm. wide; petals greenish yellow, glabrous internally, pubescent externally; fruits 4.5 cm. long; plant spinescent in juvenile stage, unarmed at maturity. Jamaica. . . . . 6. *W. flavovirens.*

A. Fruits externally stellate-pubescent or hispid, equaling or exceeding calyx; pedicels and calyx stellate-pubescent to glabrate, sometimes with few pungent hairs at apex of pedicel and base of calyx; stems and leaves lacking prickles (or few present in *W. lutea* and *W. woodsonii*); calyx usually ca. 1/2-divided (or more in *W. tulipiflora*).
  G. Fruits stellate-pubescent, hairs less than 0.5 mm. long; leaves markedly discolorous; calyx more than 1/2-divided; petals 7–10 cm. long, externally with dense, stellate pubescence throughout; stamens arising more

or less throughout length of staminal column. Lesser Antilles, 600–900 m. alt. . . . . 7. *W. tulipiflora.*

G. Fruits densely hispid with pungent hairs 2–4 mm. long; leaves somewhat discolorous to nearly concolorous; calyx about ½-divided; petals 8–13 cm. long, externally stellate-pubescent but usually glabrate toward base; stamens arising only in apical 2–3 cm. of staminal column. Costa Rica and Panama.

H. Involucel 5 cm. long, gamophyllous and spathaceous, deciduous; petals 13 cm. long, more or less orange. Veraguas, Panama, ca. 900 m. alt. . . . . 8. *W. grandiflora.*

H. Involucel 1.5–4.5 cm. long, more or less gamophyllous or 8- to 10-parted, persistent or deciduous; petals 7.5–13 cm. long, yellow or rose-lavender. Costa Rica and Panama.

I. Petals yellow; bracts of involucel more or less distinct (sometimes irregularly or basally connate); calyx stellate-pubescent and with a few pungent hairs toward base; capsules more or less pubescent internally along suture margin. 1500–2700 m. alt.

J. Involucel basally rounded, deciduous, the bracts 3, broadly ovate-sessile. Costa Rica, 1500–2500 m. alt. . . 9. *W. lutea.*

J. Involucel basally truncate, persistent, the bracts 8 or 9, narrowly triangular, with margins revolute basally. Costa Rica and Chiriquí, Panama, 1800–2700 m. alt. 10. *W. woodsonii.*

I. Petals rose-lavender; bracts of involucel more or less gamophyllous, irregularly lobed or divided; calyx stellate-pubescent, with or without pungent hairs toward base; capsules glabrous internally. 700–1700 m. alt.

K. Pedicels 1–10 cm. long at anthesis to 20 cm. long in fruit, sparsely pubescent to glabrate; leaf blades glabrate above, obscurely dentate to subentire; calyx minutely and very sparsely stellate-pubescent; staminal column 3–4 cm. long, subglabrous; fruits densely hispid, hairs 3–4 mm. long. Costa Rica, 750–1700 m. alt. . . . . 11. *W. insignis.*

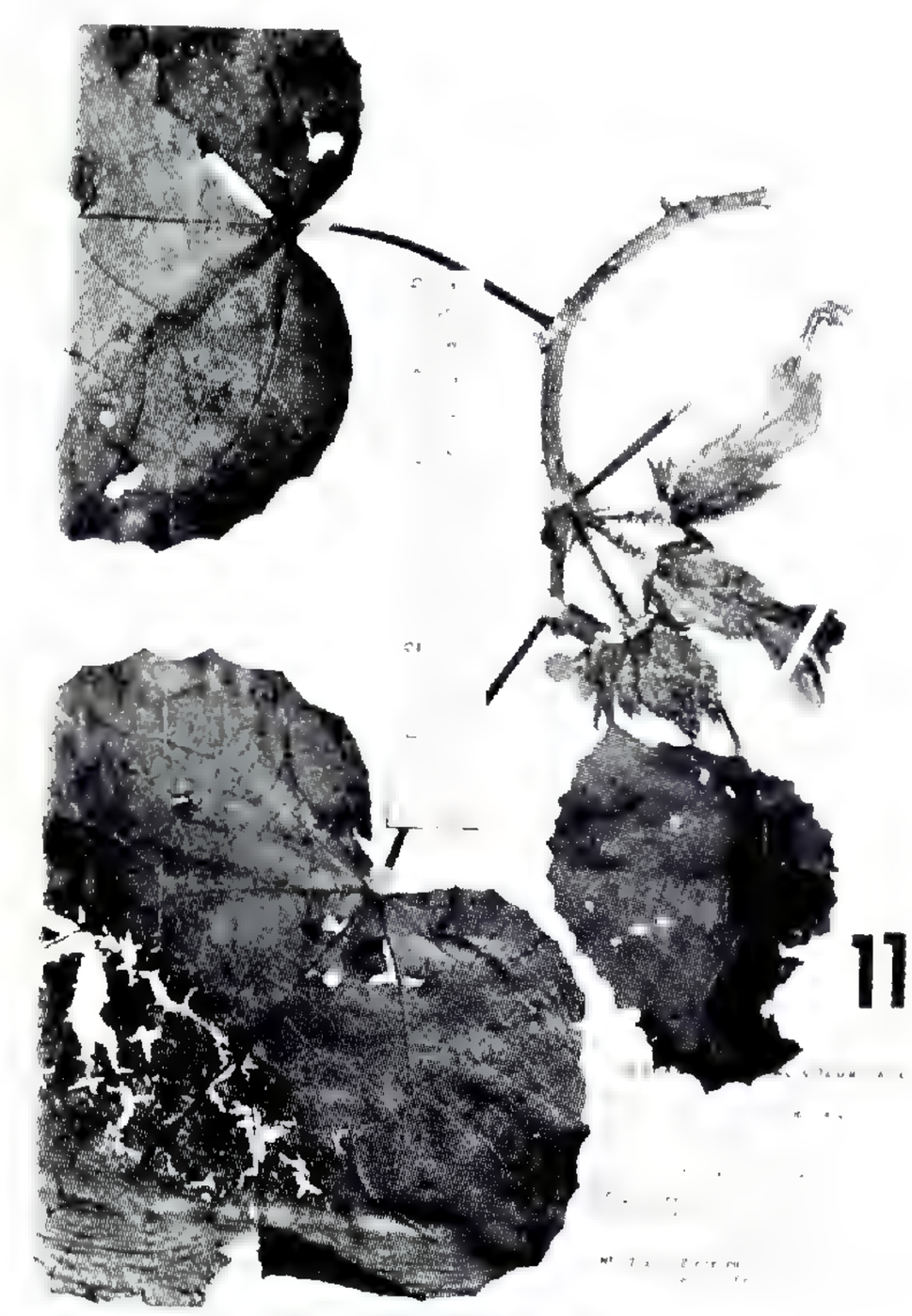
K. Pedicels 13–26 cm. long at anthesis to 30 cm. long in fruit, densely stellate-pubescent; leaf blades sparsely stellate-pubescent above, densely so on nerves, dentate; calyx minutely stellate-pubescent and with pungent hairs 1–2 mm. long toward base; staminal column 9–10 cm. long, stellate-pubescent at least basally; fruits densely hispid, hairs 2 mm. long. Coclé, Panama, 700–900 m. alt. . . . . 12. *W. cocleana.*

1. **Wercklea ferox** (Hooker) Fryxell, comb. nov. FIGURES 1, 10–14.

Hibiscus ferox Hooker, Bot. Mag. **74:** *t. 4401.* 1848. TYPE: Colombia, prope Iratcho, Dec. 1825, *Purdie s.n.* (holotype, K). Note: a mirror-image reprint of *t. 4401* occurs in Fl. Serres **4:** *t. 400.* [Oct.] 1848.

Hibiscus ferox var. *metensis* Triana & Planchon, Prodr. Fl. Novogranat. 166. 1862. TYPE: Colombia, Meta, Llano de San Martín Villavicencio, alt. 500 ft. [ca. 150 m.], Jan. 1856, *Triana & Planchon 5277* (BM; photo, NY).

Hibiscus trichomathus R. E. Fries, Kongl. Svenska Vetenskapsakad. Handl. III. **24**(2): 31. *t. 9.* 1947. TYPE: Ecuador, Prov. Napo-Pastaza, Cosanga, alt. 1900 m., 11 Jan. 1940, *Asplund 10327* (holotype, S; isotypes, S, US).



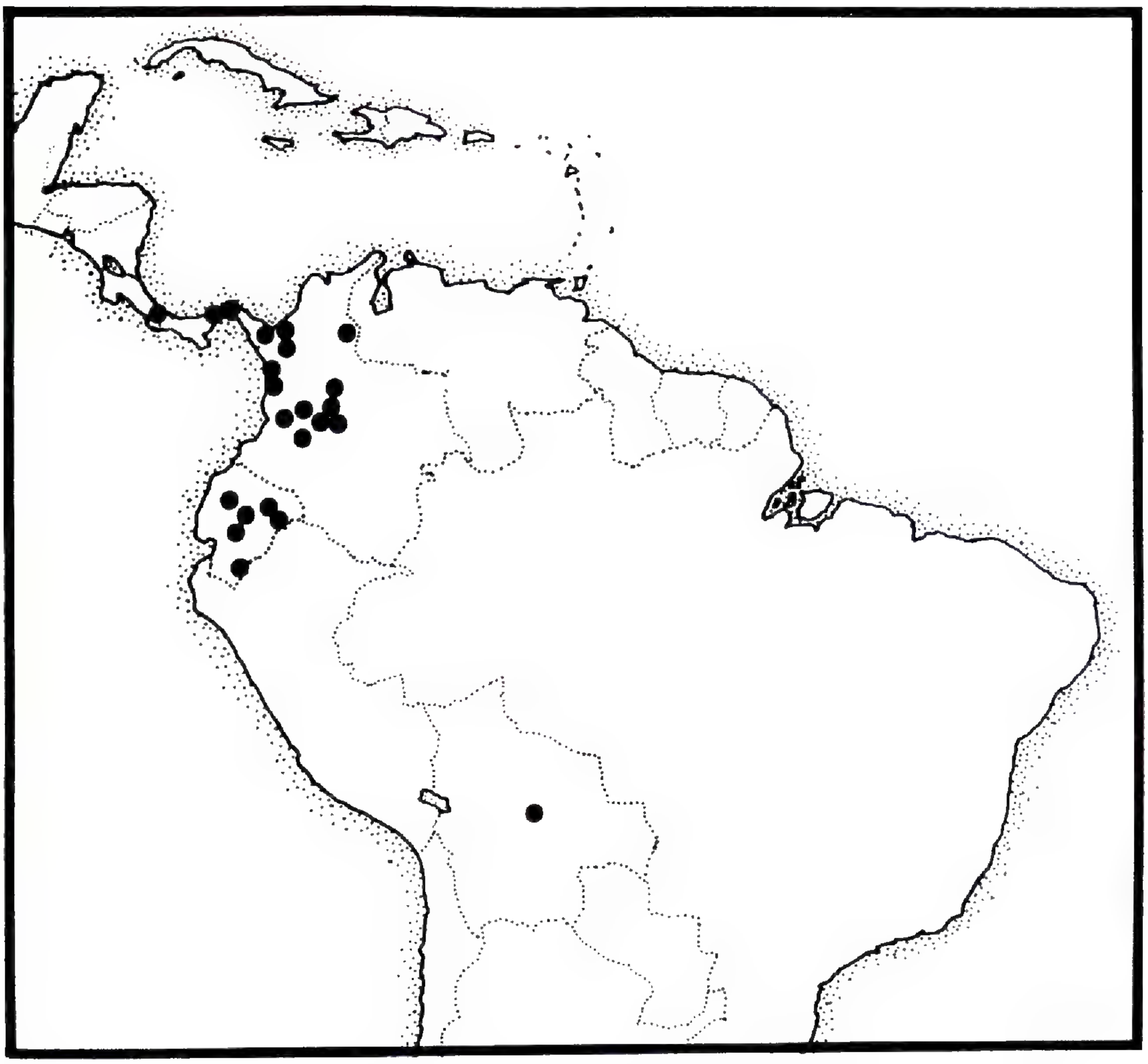
FIGURES 11–14. *Wercklea ferox:* 11, *Forero & Gentry 736,* spines absent on leaves; 12, *López & Sánchez 24,* extreme example of fasciculate flowers; 13, *Haught 5465,* showing large stipules characteristic of *Wercklea*; 14, *Steyermark & Allen 17223,* showing accrescent calyces and (in one case) enclosed fruit (cf. FIGURE 1).

Stout herb, shrub, or tree 0.5–5 meters tall; stems minutely to coarsely stellate-pubescent and also more or less aculeate, the prickles yellowish, ligneous, conical, 4–8 mm. long, 4–6 mm. broad at base. Leaf blades to at least 35 cm. long, 50 cm. broad, cordate, ovate or flabelliform to weakly lobulate, serrate (teeth often remote, sometimes spinescent), more or less acute, palmately 7- to 9-nerved, the upper surface stellate-pubescent (hairs often few armed, sometimes simple) or glabrate, with yellowish, spine-tipped prickles 2–5 mm. long on lamina between veins, the lower surface more densely and coarsely stellate-pubescent, with prickles located on principal nerves, prickles above and below sometimes sparse to absent. Petioles to 45 cm. long, stellate-pubescent and prickly like lamina, prickles sometimes few or absent. Stipules 3–5(–8) cm. long, 0.8–2.5(–4.5) cm. wide, sessile-ovate (rarely bifid), acute, minutely stellate-pubescent and with few simple hairs 1–2 mm. long especially on margins, deciduous leaving prominent scars. Pedicels in fascicles of 1 to 5 (to 9) in leaf axils, shorter than subtending petiole, 2–10 cm. long at anthesis to 13 cm. long in fruit, densely covered (especially apically) with spreading or retrorse prickles or pungent hairs 3–8 mm. long (these usually with enlarged bases) and with stellate hairs. Involucellar bracts 6 to 10, distinct (rarely gamophyllous: *von Sneidern 5422, Kalbreyer 1303*), 1.5–3(–5) cm. long, 4–12 mm. wide, lanceolate, acute, minutely pubescent and with some pungent hairs. Calyx 2.5–3.5(–5.5) cm. long at anthesis to 8(–13) cm. long in fruit, gamosepalous and spathaceous becoming inflated (fusiform) and reticulate veined, 10-fluted, externally densely beset with spinose-tipped pungent hairs 3–4(–10) mm. long (these usually with enlarged bases), internally glabrous, 5-lobed; lobes 6–9(–20) mm. long, triangular. Petals 6–9 cm. long, .5–1.5 cm. wide, yellow, externally densely covered with minute, peglike hairs and with at least few stellate hairs distally, reflexed to form salverform corolla (rarely (*Haught 5465*) corolla 10 cm. long, campanulate). Staminal column glabrous, shorter than to equaling petals but often appearing exserted when petals reflex, staminiferous in distal 1.5 cm. Styles slightly exceeding androecium, barely divided, with 5 capitate, purplish, hairy stigmas. Fruit 3–5 cm. long, 1–2 cm. in diameter, a cylindrical or oblong capsule, essentially wingless, wholly enclosed by inflated calyx, glabrous internally and externally, beak reduced to 0.5–2 mm. long. Seeds numerous, 2.5–3 mm. long, phaseoloid, blackish, minutely puberulent, hairs less than 0.1 mm. long.

DISTRIBUTION. Costa Rica to Bolivia (MAP 1), sea level to 1000(–2000) m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** TALAMANCA: bords du Buridikur, *Pittier 9404* (US). **Panama.** PANAMÁ: tributary of Río Chagres, 5 mi. [8 km.] SW. of Cerro Brewster, *Lewis et al. 3431* (COL, MO, UC). CANAL ZONE: forest between Peluca Hydrographic Station and Quebrada Peluca, along Río Bo-querón, *Steyermark & Allen 17223* (BR, CAS, K, MO, S, UC); gravel bench of Chagres at Alajuela, *Pittier 2345* (BM, US). COLÓN: vic. of Portobelo, *Croat 33571* (MO, pf[1]); along river ca. 4 mi. [6.5 km.] SW. of Portobelo, *Croat*

[1]The acronym "pf" refers to the author's herbarium.



MAP 1. Distribution of *Wercklea ferox*.

14108 (MO); 10 mi. [16 km.] SW. of Portobelo, 2–4 mi. [3.2–6.5 km.] from coast, *Liesner 1102* (F, MO, NY); Río Viejo, vic. of Puerto Pilón, *Allen 4098* (MO, NY, S); mouth of Río Piedras, beach and adjacent area, *Lewis et al. 3164* (COL, DUKE, K, MO, UC); Río Guanche, between María Chiquita and Portobelo, 1–5 mi. [1.6–8 km.] up river from hwy., *Foster & Vocelka 2192* (DUKE, MO); Río Guanche, 1–4 km. upstream from Portobelo Rd., *A. Gentry 8801* (F, MO, pf); Río Guanche, *D'Arcy 9726* (MO, pf); Caña and vic., *Williams 819* (CAS, NY, US). DARIEN: Mannene to mouth of Río Coasí, *Kirkbride & Bristan 1421* (NY). **Colombia.** NORTE DE SANTANDER: región del Sararé, Hoya del Río Cubugón, El Indio, *Cuatrecasas 13093* (F, US (3 sheets)). ANTIOQUÍA: Chigorodó, carretera a Turbo, *García-Barriga 17653* (NY, US); selva pluvial, carretera al mar cerca de Villa Arteaga, *López & Sánchez 24* (US); Marinilla, *Kalbreyer 1303* (K). SANTANDER: region about La Paz, 25 km. NE. of Velez, moist pasture, Canta Ranas, 5 km. N. of La Paz, *Fassett 25177* (CAS, US). CHOCÓ: Bahia Utria, in forest along Río Sampechi, *Haught 5512* (NY, US); Río Nuquí, *Haught 5465* (K, US); Río El Valle cerca de la desembarcadura al Río Miniquía, entre este y el Río Mutatá, terreno pedregoso, lecho seco del río, *Forero & Gentry 736* (MO); carretera Tutunendo–El Carmen, entre kms. 135 y 120, Alto. R. Atrato, *Forero et al. 6162* (COL, MO, pf); 6 km.

W. of Siete on Medellín–Quibdó Road, 38 km. W. of Bolívar, *Gentry & Rentería 23712* (COL, MO, pf). CUNDINAMARCA: zwischen Guayabetal und Manzanares, Cordillera oriental, *Vogel 55* (US); Nocaima–Hacienda Tobia, *García-Barriga 10576* (US). TOLIMA: El Fresno, bosque abierto, *Cuatrecasas 9378* (F, US). META: Río Manzares Valley, 22 km. W. of Villavicencio, subtropical forest, *Grant 996* (US); along Río Guatiquía near Villavicencio, *Killip 34414* (US). VALLE: Río Bravo, NW.(?) of Darien, edge of thick woodland, *Robinson 125* (K, US); Río Digua valley, Chorrera La Elsa, densely forested valley, *Killip 34805* (US). CALDAS: Pueblo Rico, La Selva, *von Sneidern 5422* (S, pf). **Ecuador.** NAPO-PASTAZA: Cosanga [77°52′W., 0°35′S.], hillside W. of town, *Boeke & McElroy 379* (NY (unicate—topotype of *Hibiscus trichomathus*)); near Baeza [15 km. N. of Cosanga] on road to Tena, *Davis 366* (S); road Baeza–Tena, ca. 5 km. from Baeza; alt. 200 m., *Øllgaard & Balslev 10242* (AAU). PICHINCHA: road Aloag to Santo Domingo, Toáchi at confluence of Río Pilatón and Río Toáchi, *Sparre 15126* (S, pf). BOLÍVAR: below Balzapamba, *Haught 3314* (NY, S, UC, US). LOS RÍOS: Puembo, 34 km. E. de Quevedo, Río Quevedo, arroyo, *Gonzáles & Gilmartin 11* (MO). ZAMORA-CHINCHIPE: Zamora, rain forest, *Harling 5932* (S, pf). **Bolivia:** Cochabamba, Chimore [64°53′W., 16°50′S.], km. 180, wet slopes at forest edge, *Cárdenas 2151* (US (2 sheets)).

Wercklea ferox is distinctive in having its flowers and fruits in fascicles of 1 to 5 (to 9) per axil, and in having glabrous fruits completely enclosed by inflated calyces and borne on relatively short pedicels. Its petals are the smallest of the yellow-flowered species.

Wercklea ferox always grows in wet habitats, frequently near rivers and at relatively low altitudes. It has often been collected near sea level, at or near the mouths of rivers; it also occurs in wet forests and forest margins up to 1000 (rarely 2000) meters altitude.

Collectors' notes variously characterize it as a "large herb," a "coarse herb," a shrub, or a small tree; sometimes it is described as having "succulent" stems. Herbarium specimens reveal that relatively young stems (which more commonly make their way into a plant press) often are either hollow or have soft pith; older stems are clearly woody.

In addition to noting the growth habit and prickly herbage, collectors also commonly record the striking color contrasts presented by plants of this species. Because these colors are generally poorly preserved in dried specimens, they deserve special comment. The corolla is usually said to be yellow (or bright or golden yellow), sometimes yellow with a reddish throat, sometimes orange. The calyx and involucel are usually noted to be red or bright red. The young stems, the petioles, and the main veins of the lower surface of the leaves are also described as red or sometimes as pink. All in all, the plant seems to merit the description "very conspicuous" (*Haught 3314*). The flowers are said to be odorless (*Gentry 8801*).

That Cárdenas found this species in Bolivia draws attention to a significant hiatus in its distribution in Peru (MAP 1). Either the plant occurs in Peru but has escaped detection because it is found in poorly collected areas, or the hiatus is real and a disjunction exists; a third alternative is that the

Bolivian material represents a distinct taxon. My initial view, on first examining the Cárdenas specimens from Bolivia, was that they represent a distinct (undescribed) species. A fuller understanding of the variability found within *Wercklea ferox*, however, makes it clear that the Bolivian material cannot be distinguished from this species, at least on the basis of the material available. Unfortunately, fruiting specimens from Bolivia have not yet been collected.

Wercklea ferox is both the most widely distributed and the most variable species of the genus. For example, the prickles that are so distinctive of the species are not always present. On the leaves, especially, they may vary from dense to absent (FIGURES 11, 13). There are usually at least some prickles present on the older stems, but these stems are only rarely represented in herbarium specimens. Even on the calyx and pedicel, where dense, spreading prickles are characteristic, these hairs are sometimes reduced to simple pungent hairs without swollen bases. Other structures (calyx, involucel, pedicels, stipules) are quite variable in size, but the overall pattern appears to be one of a single, highly variable species.

2. **Wercklea pseudoferox** (Hochr.) Fryxell, comb. nov. FIGURE 15.

Hibiscus pseudoferox Hochr. Annuaire Conserv. Jard. Bot. Genève **4:** 123. 1900. TYPE: Nov. Granada [Colombia], [Norte de Santander], Ocaña to Pamplona, Salazar, 5000–6000 [ft.] [1500–1800 m.], 26 Mar. 1879, *Kalbreyer 1037* (lectotype, K; isotype, K).

"Half-shrub 4–7 ft." [1.2–2.1 m.] tall; stems stellate-pubescent and sparsely prickly, the prickles conical and retrorsely curved, 2–2.5 mm. long, 1.5 mm. in diameter at base. Leaf blades to at least 28 cm. long, 35 cm. broad, cordate, ovate, sharply serrate (teeth spinescent), acute, palmately 7-nerved, discolorous, the upper surface with appressed simple hairs and few 2- (or more-)armed stellate hairs, and with few spine-tipped prickles on lamina between veins, the lower surface densely stellate-pubescent and with few spine-tipped prickles on principal veins. Petioles 1/2–2/3 length of blade, densely stellate-pubescent with few longer simple hairs and with occasional conical prickles to 3 mm. long. Stipules 8–12 mm. long, 3–6 mm. wide, lance-ovate, acute, stellate-pubescent externally, antrorsely strigose within. Pedicels solitary in leaf axils, exceeding subtending petiole, ca. 20 cm. long at anthesis to 34 cm. long in fruit, stellate-pubescent and with spine-tipped prickles 1–2 mm. long. Involucel 2–2.5 cm. long, of 8 or 9 bracts; bracts distinct, 4–6 mm. wide, lanceolate, acute, stellate-pubescent, with pungent hairs at very base. Calyx 6 cm. long at anthesis to 9 cm. long and inflated in fruit, ca. 1/3-divided, prominently ribbed, densely stellate-pubescent throughout and with spine-tipped prickles especially on ribs of lower half; lobes 3-ribbed, triangular, acute, 10–12 mm. wide at sinus. Petals 10.5 cm. long, "brown-yellow," stellate-pubescent externally. Staminal column 10.5 cm. long, glabrous, antheriferous in distal 3 cm.; filaments 3–5 mm. long. Style glabrous, exceeding staminal column by 7 mm., 5-parted for distal 2 mm.; stigmas capitate, 3 mm. in diameter, with long (1 mm.) hairs. Capsule included in calyx, 5.5 cm. long, essentially glabrous.

15

16

17

18

FIGURES 15–18: 15, *Wercklea pseudoferox* (*Kalbreyer 1037*); 16, *W. hottensis* (*Ekman 9223*); 17, 18, *W. horrida* (*Ekman 14115*).

DISTRIBUTION. Colombia (MAP 2); known only from the type locality.

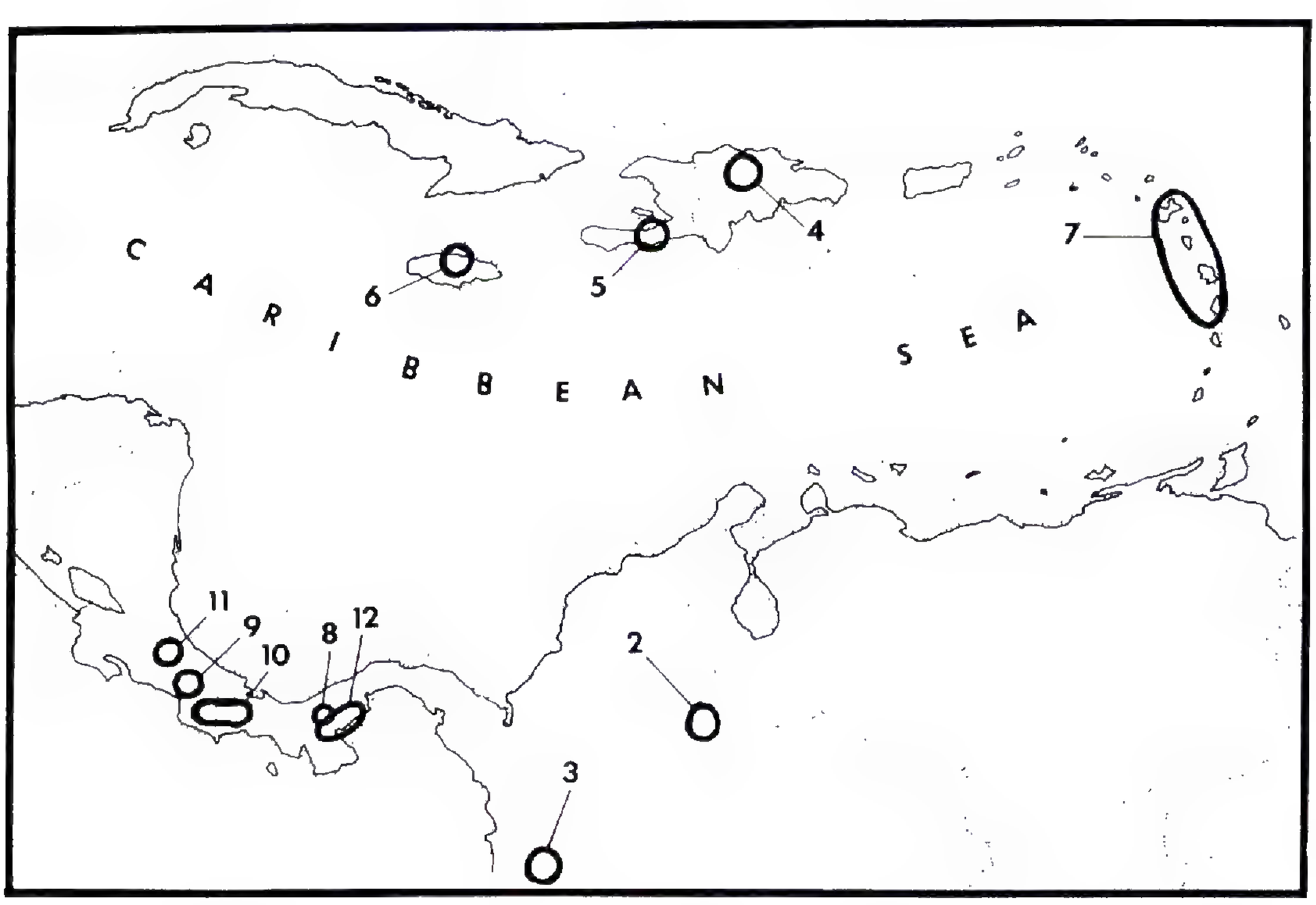
Wercklea pseudoferox has its closest affinity to *W. ferox*, as the name suggests, but is characterized by inflated, spathaceous calyces enclosing the fruit, coupled with solitary, very long pedicels and a relatively small involucel.

3. **Wercklea magnibracteata** Fryxell, sp. nov. FIGURES 21, 22.

Wercklea arborescens, stellato-pubescens; foliis plus latioribus quam longioribus, pentangularibus vel 5-lobulatis, lobulis acutis; stipulis ovatis, acutis, 40–52 mm. longis, 20–25 mm. latis; pedicellis florentibus ca. 19 cm. longis; bracteis involucellorum 3–6, distinctis, ovatis, 40–45 mm. longis, 16–27 mm. latis; calycibus 6–9.5 cm. longis, accrescentibus atque inflatis fructus includentibus; capsulis glabris.

TYPE: Colombia, Antioquía, 34 km. W. of Dabeiba on road to Mutatá, alt. 420 m., steep roadside cliff; weak tree 8 m., flowers yellow, all closed at mid-day, 8 Oct. 1977, *Gentry & León 20267* (holotype, MO; isotypes, COL, pf).

Tree to 8 meters tall; stems densely stellate-pubescent and with occasional prickles ca. 1 mm. long. Leaf blades to at least 24 cm. long, 28 cm. wide, cordate, weakly 5-angled or -lobulate, margin remotely serrate, lobes acute, palmately 9-nerved, the upper surface with scattered, minute, stellate hairs



MAP 2. Distribution of species of *Wercklea* (excluding *W. ferox*). Species numbered as in text: 2, *W. pseudoferox;* 3, *W. magnibracteata;* 4, *W. horrida;* 5, *W. hottensis;* 6, *W. flavovirens;* 7, *W. tulipiflora;* 8, *W. grandiflora;* 9, *W. lutea;* 10, *W. woodsonii;* 11, *W. insignis;* 12, *W. cocleana.*

FIGURES 19–22: 19, *Wercklea grandiflora* (*Nee 9842*); 20, *W. insignis* (*Rowlee & Stork 286;* see FIGURE 6); 21, 22, *W. magnibracteata* (*Gentry & León 20267*).

(these sometimes few armed and antrorsely oriented) and with veins more densely pubescent, the lower surface stellate-pubescent (densely so and yellowish when young). Petioles shorter than blades, with pubescence like that of stem. Stipules 40–52 mm. long, 20–25 mm. broad, ovate, acute to acuminate (rarely bifid), minutely stellate-pubescent externally, antrorsely strigose internally, parallel veined. Pedicels solitary or paired in leaf axils, ca. 19 cm. long at anthesis (equaling or exceeding subtending petiole?), stellate-pubescent and with pungent hairs 2 mm. long especially toward distal end. Involucel 40–45 mm. long, of 3 to 6 bracts; bracts distinct, lanceolate to ovate, acute, 16–27 mm. broad, minutely stellate-pubescent and with few pungent hairs on veins near base. Calyx 6 cm. long at anthesis to 9.5 cm. long and inflated in fruit, ca. 1/3-divided, prominently ridged, densely hispid, especially on nerves, with pungent hairs 1–3 mm. long. Petals yellow, ca. 10 cm.(?) long, externally stellate-pubescent distally. Capsule ca. 4 cm. (or more?) long, glabrous, reticulate veined, weakly winged.

DISTRIBUTION. Colombia (MAP 2); known only from the type location.

Wercklea magnibracteata is most clearly allied to *W. pseudoferox*, as is indicated by its position in the key. It is allied generally with those species having glabrous capsules, and more specifically with those (*W. ferox* and *W. pseudoferox*) having accrescent, spathaceous calyces. However, it also shares certain characters (pubescence pattern, large stipules and involucel) with *W. grandiflora*, further indicating ties between the glabrous- and hispid-fruited species and supporting the integrity of *Wercklea* as here delimited. *Wercklea magnibracteata* is distinctive for its large, involucellar bracts (whence the specific epithet; see FIGURE 22), which are distinct and relatively few in number.

4. **Wercklea horrida** (Urban) Fryxell, comb. nov. FIGURES 9, 17, 18.

Hibiscus horridus Urban, Symb. Antill. **7:** 280. 1912. TYPE: Sto. Domingo, Prov. Barahona, Gipfel des Noche Buena Berges, 1800 m., Sept. 1911, *Fuertes 1074* (lectotype, NY; isotype, A); *Fuertes 1128* (syntype).

Stout herb or tree 3–8 meters tall; stems stellate-pubescent and with relatively narrow conical prickles 3–7 mm. long. Leaf blades to at least 20 cm. long, 28 cm. wide, cordate, more or less orbicular, often 5- to 7-lobed, prominently dentate (teeth often spine tipped), acute or obtuse, palmately 7-nerved, the upper surface sparsely and minutely stellate-pubescent to glabrate and with narrow prickles 2–7 mm. long on lamina between veins, the lower surface stellate-pubescent and with narrow prickles 5–8 mm. long abundantly on principal and secondary veins, somewhat discolorous. Petioles to 22 cm. long, stellate-pubescent and with narrow prickles 4–8 mm. long. Stipules not seen, scars 10–12 mm. long. Pedicels 1 or more in leaf axils, shorter than subtending petiole (up to 7 cm. long), with stellate pubescence and densely beset with narrow prickles 4–9 mm. long. Involucel 10–18 mm. long, ca. 10-parted; bracts lanceolate, acute, 1.5–3(–6) mm. wide, with fewer hairs and prickles than pedicel or calyx. Calyx 2–3.5 cm. long at anthesis, tubular,

ca. 1/4-divided, stellate-pubescent and densely beset with narrow prickles 3–10 mm. long. Petals 6–9 cm. long, 1.5–2.3 cm. wide, "rose" or "red-brown," stellate-pubescent internally and externally except toward base, reflexed making corolla salverform. Staminal column about equaling petals but appearing exserted when petals reflex, glabrous, staminiferous in distal 1/2, filaments 2–6 mm. long. Stigmas slightly exserted from staminal column, capitate, hairy. Fruits 2–3 cm. long, ovoid, wingless, 5-loculed, glabrous and prominently reticulate veined externally, pubescent internally with hairs 2–3 mm. long. Seeds 2.8 mm. long, blackish, glabrous, reniform.

DISTRIBUTION. Dominican Republic (MAP 2), 1000–1800 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Dominican Republic.** Banks of Arroyo de la Sal, Loma de la Sal, Jarabacoa, *Bro. Alain Liogier 11399* (IJ, NY). BARAHONA: Montiada Nueva, forested hillslopes SE. of Polo, trail to Paraíso, S. of Montiada Nueva, *Howard & Howard 8543* (BM, GH, NY, S, US); between Monteada Nueva and Loma Alta, *Howard 12312* (A, BM, BR, US). LA VEGA: Cordillera Central, road Costanza to Zarabacoa at El Río, *Ekman H14115* (NY, S, US).

Wercklea horrida is distinctive for its very small (2–3 cm. long) fruits and is further characterized by its combination of glabrous fruits, rose-colored corolla, and calyx not enclosing the fruit. It is also notable for its conspicuously armed herbage, as its name suggests.

5. **Wercklea hottensis** (Helwig ex Urban) Fryxell, comb. nov. FIGURE 16.

Hibiscus hottensis Helwig ex Urban, Ark. Bot. **22A**(8): 74. 1928. TYPE: Haiti, Massif de la Hotte, central group, St. Louis du Sud, Bonnett Carré, 900 m., quite common, 2 Nov. 1927, *Ekman 9223* (lectotype, S; isotypes, IJ, US).

Shrub 2–3 meters tall; stems with yellowish prickles 3–6 mm. long, otherwise glabrate; young stems with soft pith. Leaf blades to at least 18 cm. long, 23 cm. wide, cordate, more or less orbicular, obscurely 7-lobed, prominently dentate (teeth spine tipped), acute, palmately 7- to 9-nerved, the upper surface glabrate and with narrow prickles 1.5–5.5 mm. long on lamina between veins, the lower surface sparsely stellate-pubescent (especially on veins) and with narrow prickles 1.5–5.5 mm. long on principal and secondary veins, discolorous. Petioles to 15 cm. long, sparsely stellate-pubescent and with narrow prickles 4–6.5 mm. long. Stipules not seen, stipule scars 10–12 mm. long. Pedicels solitary in leaf axils, longer than subtending petiole, up to 20 cm. long at anthesis to 28 cm. long in fruit, glabrate proximally to densely and minutely stellate-pubescent distally and with narrow, yellowish prickles 2–4 mm. long. Involucel 18–25 mm. long, more or less gamophyllous, irregularly 6- to 10-lobed, sometimes splitting to base in 1 or 2 places, many veined from base, glabrate or stellate-pubescent and spinescent on veins. Calyx 3 cm. long at anthesis to 4.5 cm. long in fruit, prominently 15-nerved, ca. 1/4-divided, stellate-pubescent and beset with narrow prickles 3–6 mm. long (principally on nerves). Petals "pale flesh colored" (yellowish when

dry), 6–8 cm. long, prominently parallel veined, minutely stellate-pubescent in distal ½, glabrous in proximal ½. Staminal column about equaling petals, staminiferous only near apex. Fruits 5 cm. long, oblong-ovoid, wingless, 5-loculed, glabrous externally, pubescent internally, the hairs 2–3 mm. long, delicate, whitish. Seeds 2.5 mm. long, blackish, glabrous, reniform.

DISTRIBUTION. Haiti (MAP 2), ca. 1000–1200 m. alt.

ADDITIONAL SPECIMEN EXAMINED. **Haiti.** DÉP. DU SUD: pr. Donyette (int. Port à Piment et Aut Anglais), *Ekman H482* (S).

Wercklea hottensis is characterized by its combination of rose-colored flowers, glabrous fruits (not enclosed by an inflated calyx), long pedicels, and more or less gamophyllous involucels.

6. **Wercklea flavovirens** Proctor, sp. nov. FIGURES 7, 8.

Wercklea arborescens, sparse stellato-pubescens, spinescens juventute, postea inermis; foliis plus latioribus quam longioribus, 5-lobatis, remote serratis; stipulis ovatis, acutis, 20–45 mm. longis, 5–25 mm. latis; pedicellis usque ad 9.5 cm. longis; bracteis involucellorum ca. 6, ovatis, basaliter imbricatis, 25–30 mm. longis, usque ad 12 mm. latis; calycibus 25–30 mm. longis; petalis flavo-virentibus, 8–9 cm. longis, ca. 1.5 cm. latis; capsulis 4.5 cm. longis, extus glabris, intus hirsutis.

TYPE: Jamaica, Portland Parish, McRobert Patent, in John Crow Mtns., ca. 6 mi. [9.7 km.] by road S. of Sherwood Forest, secondary rain forest over limestone, ca. 1150 ft. [350 m.], 27 Mar. 1979, *Watts, Podzorski, & Kelly JCM1548* (holotype, IJ).

Spiny herb or unarmed tree, 5–6 meters tall; young stems densely covered with pungent, yellowish spines 5–11 mm. long, 0.5–1.5 mm. in diameter, underlying stellate pubescence sparse; mature stems unarmed, sparsely and minutely stellate-pubescent. Leaf blades to at least 28 cm. long, 35 cm. wide, palmately 5-lobed, basally cordate, remotely serrate (teeth spinescent in leaves of young plants), acute, palmately 7- to 9-nerved, minutely stellate-pubescent (especially on nerves) to glabrate above and beneath, in young plants also with yellowish, spine-tipped prickles 3–9 mm. long on lamina between veins above and on principal nerves beneath. Petioles to 15 cm. long, with pubescence like that of stem. Stipules 20–45 mm. long, 5–25 mm. wide, (lanceolate to) sessile-ovate, acute, minutely and sparsely pubescent (especially on margin), the hairs simple or stellate, deciduous leaving prominent scars. Pedicels solitary in leaf axils, to 9.5 cm. long, minutely stellate-pubescent. Involucel of ca. 6 bracts; bracts ovate, overlapping basally, 25–30 mm. long, up to 12 mm. broad, acute, minutely pubescent to glabrate, deciduous in fruit. Calyx 25–30 mm. long, minutely stellate-pubescent, ca. ½-divided, lobes 3-nerved. Petals greenish yellow, 8–9 cm. long, ca. 1.5 cm. broad, externally with scattered, stellate pubescence except toward base, internally glabrous. Staminal column subequal to petals, glabrous, staminiferous in distal ½; filaments 3–4 mm. long. Style slightly exceeding androecium, barely divided, with 5 capitate,

pallid, hairy stigmas. Fruit an ovoid or fusiform capsule, 4.5 cm. long, 2.7 cm. in diameter, pentangular, acute or slightly beaked, externally glabrous and obscurely reticulate veined, internally densely hirsute, the hairs whitish, 3–5 mm. long. Seeds numerous, reniform, 3 mm. long, glabrous.

DISTRIBUTION. Jamaica (MAP 2); known from a single locality.

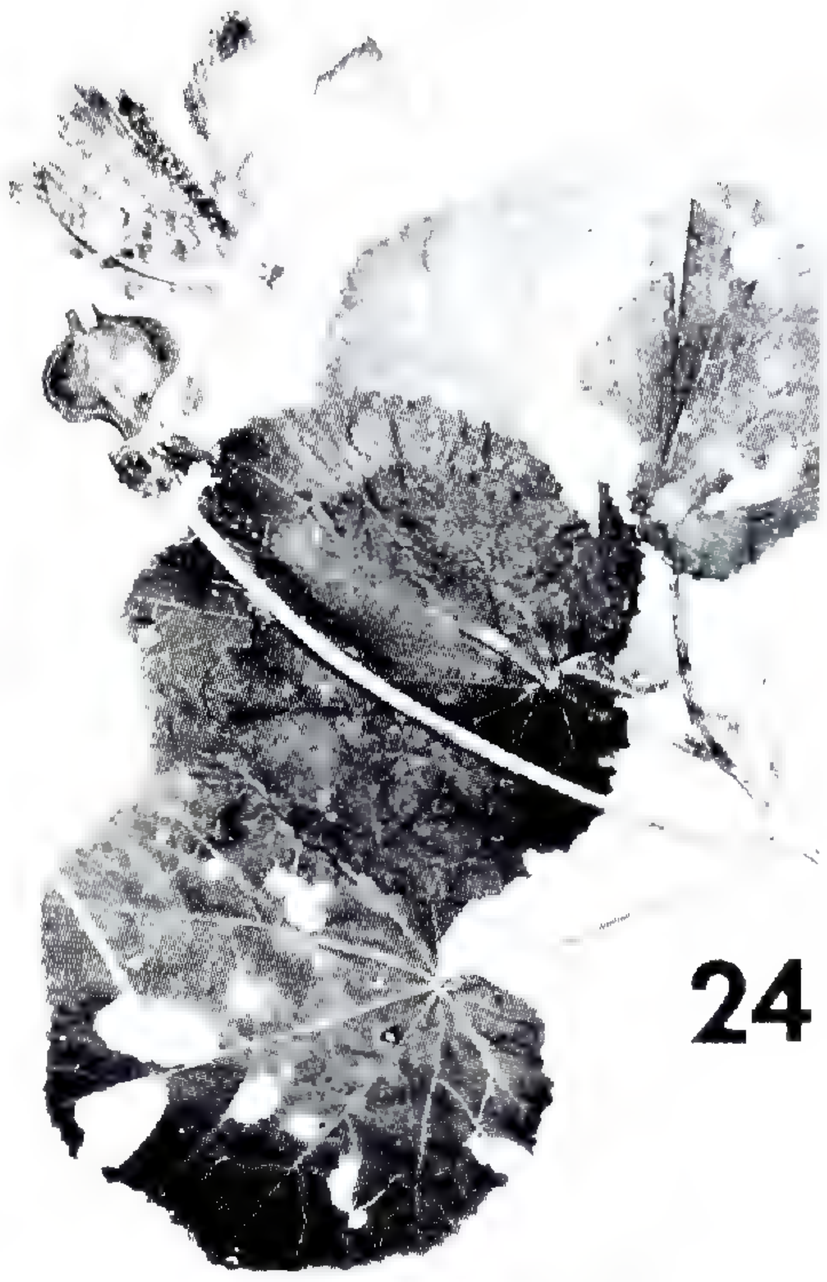
ADDITIONAL SPECIMENS EXAMINED. **Jamaica.** PORTLAND PARISH: in John Crow Mtns., ca. 6 mi. [9.7 km.] S. of Sherwood Forest, [juvenile specimen] *Proctor 36707* (IJ), [fruiting specimen] *Proctor 37837* (IJ).

Wercklea flavovirens, unusual in combining a juvenile form that is heavily spinescent with a mature form that is unarmed, is perhaps similar in this combination to *W. woodsonii* ("spined when young"—*Heithaus 411*). It has its affinity, both morphologically and geographically, with *W. horrida* and *W. hottensis,* from Hispaniola, as is indicated by its position in the key. The latter two species, however, are notably spinescent as mature plants. *Wercklea flavovirens* is further distinguished by its relatively narrow, greenish yellow petals (whence the specific epithet) and by its large fruits (exceeding the calyx) that are completely glabrous externally. Its leaves are more prominently lobed than those of most species of *Wercklea,* a characteristic that it shares with *W. horrida.*

7. **Wercklea tulipiflora** (Hooker) Fryxell, comb. nov. FIGURES 2, 23, 24.

Hibiscus tulipaeflorus Hooker, Ic. Pl. II. **4:** *tt. 707, 708.* 1845. TYPE: Isl. Dominica, Couliaban Mtns., *Imray 251* (K (2 sheets)).
Abelmoschus tulipaeflorus (Hooker) Walp. Rep. Bot. Syst. **5:** 92. 1845.
Hibiscus tulipiferus Regel, Catal. Pl. Horto Arsakov. 71. 1860.(?)

Tree 3–10 meters tall; stems minutely pubescent to glabrate. Leaf blades to at least 20 cm. long, 30 cm. broad, deeply cordate, indistinctly pentagonal or suborbicular, irregularly and coarsely crenate-dentate, obtuse or subacute, palmately 7- to 9-nerved, markedly discolorous, upper surface sparsely pubescent to glabrate, lower surface minutely and sparsely to densely stellate-pubescent. Petioles shorter than to longer than blades, very sparsely stellate-pubescent to glabrate. Stipules (1–)2–4 cm. long, 1–2.7 cm. wide, ovate to semicircular, acute to subacute, sometimes recurved, stellate-pubescent, deciduous. Pedicels 6–27 cm. long, stout (5–6 mm. in diameter) and woody in fruit, articulated 0.2–15 mm. above base, glabrate to stellate-pubescent, more densely so at apex. Involucel 2–5 cm. long, 6- or 7-parted; bracts distinct, spreading, 6–13 mm. wide (narrower at insertion), lanceolate to subrhomboid, acute, several nerved, sparsely stellate-pubescent. Calyx 3–5.5 cm. long, more than ½-divided, sparsely and very minutely stellate-pubescent; lobes 3- to 5-nerved, ovate, acute, 1.5–2 cm. broad at sinus, 2–3.5 cm. long. Petals 7–10 cm. long, ca. 3 cm. broad, pale yellow, externally stellate-pubescent throughout, sparsely pubescent internally. Staminal column 5.5–7 cm. long (somewhat shorter than petals), staminiferous nearly throughout length; filaments 1–4 mm. long (progressively shorter upward). Stigmas 5, capitate,



FIGURES 23–26. 23, 24, *Wercklea tulipiflora:* 23, *Hodge & Hodge 1879,* in flower; 24, *Duss 2323* (see FIGURE 2), in fruit. 25, 26, *W. lutea:* 25, *Collado s.n.,* in flower; 26, *Standley 38339,* in fruit.

ca. 2 mm. in diameter, densely yellow-villous; style branches free for 1–2 mm., exceeding staminal column. Fruit a prominently winged capsule, usually stipitate and broadly obovoid, 4–5.5 cm. long, almost as broad, with beak 4–6 mm. long, densely stellate-pubescent and reticulate veined externally, internally pubescent on suture margin, the hairs mostly simple, 2–4 mm. long; fruits "turning black when ripe" (*Ramage s.n.*).

DISTRIBUTION. Lesser Antilles (MAP 2), 600–900 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Guadeloupe:** "gombo grand bois," *Duss 2323* (NY, US); between St. Cloud and Bains Jaunes on trail to Soufrière, *Howard 11803* (A). BASSE-TERRE: Massif de la Soufrière, début du chemin menant vers le Pas du Roi, *Sastre, Fournet, & Clairon 2851* (A (2 sheets)), MO); trail to Morne la Soufrière, *Holdridge 427* (NY); chemin menant à la 1ère chute du Carbet, 2° pente, *Sastre & Sastre 2044* (A). **Dominica:** en monte Sulfureo, *Duchassaing s.n.* (K); Laudat, 19 April 1888, *Ramage s.n.* (K); vic. of Freshwater Lake, near Laudat, *Smith 10234* (IJ, NY, S); St. George Parish, Freshwater Lake, *Nicolson 1957* (DUKE); St. George, Freshwater Lake Area, S. face of Micotrin, mossy forest, *Wasshausen & Ayensu 311* (IJ, SMU); on slopes of Morne Macaque (Micotrin), *Wilbur et al. 8251* (DUKE); Freshwater Lake in elfin woodland, *Beard 235* (A, K, MO, NY, UC); between Freshwater Lake and Boeri Lake, *Wilbur et al. 8215* (DUKE, TEX); rainforest on precipitous slopes of Morne Colla Anglais, *Hodge 549* (NY), *Hodge 1127* (GH (2 sheets)); rainforest borders between Laudat and Freshwater Lake, *Hodge & Hodge 1879* (GH). Without exact locality, *Cooper 40* (DUKE, GH, NY). **Montserrat:** Chance's Mtn., summit area, *Proctor 19109* (A, IJ); Chance's Mtn., in elfin woodland, apparently confined to this summit, *Beard 447* (A, K, MO); forest at caldera ridge summit, Central Mtn. range, *Howard & Howard 17513* (A).

According to Stafleu (1967, pp. 215, 492), Hooker's name was published in May, 1845, and Walpers's name in November, 1845. Moreover, Walpers cited Hooker, indicating that the basionym was provided by Hooker and not by Walpers, as was stated by Kearney (1955, p. 283, note 29).

This species occurs in the Lesser Antilles in Guadeloupe, Dominica, St. Lucia, and Montserrat (cf. Stehlé, 1943), where it is evidently rare. It occurs at altitudes of 600–900 meters in wet forests or elfin woodlands.

Kearney (1955, p. 283, note 29), presumably following Hochreutiner (1900), cited *Hibiscus marmoratus* Lem. (Ill. Hort. **3:** *t. 82.* 1856) as doubtfully synonymous with *H. tulipaeflorus.* The plate represents *H. lavateroides* Moric., however, not *Wercklea tulipiflora.* The plate in *Flore des Serres* (1856, *t. 1159*) is not identical, although it is clearly based on the same plant as the plate in *Illustration Horticole.* Kearney (*loc. cit.*) also cited a specimen from Santiago de las Vegas, Cuba (*Baker 102* (K, UC)) as a probably cultivated specimen of *W. tulipiflora,* but this specimen is, in fact, *H. indicus* (Burman f.) Hochr.

The corolla of *Wercklea tulipiflora,* according to Hooker's original description, is rose colored, whereas Stehlé (1943) stated that the flowers were white. The labels of all the above-cited specimens that record flower color give it as yellow. It is likely that the fresh flowers are pale yellow and fade to rose, and that this pattern results in the discrepancy noted.

Wercklea tulipiflora is unique in the genus and is set apart from the other species by a series of characters, including stellate-pubescent fruits, complete absence of prickles or pungent hairs, deeply divided calyx, subrhomboid involucellar bracts, markedly discolorous leaves, petals externally pubescent over the entire surface, and androecium staminiferous nearly throughout its length.

A collector's note (*Hodge 1127*) states "rope made of bark to tie bundles," another example of the use of bast fibers in the Malvaceae for this purpose.

8. **Wercklea grandiflora** Fryxell, sp. nov. FIGURE 19.

Wercklea arborescens, stellato-pubescens; foliis plus latioribus quam longioribus, infra tomentosis, leniter pentangularibus, angulis subacutis; stipulis late rotundatis, obtusis vel acutis, 13–30 mm. longis, 12–21 mm. latis; pedicellis florentibus 13 cm. longis; involucellis 5 cm. longis, gamophyllis atque spathaceis, deciduis; calycibus 3.5–6.5 cm. longis, circa semi-divisis; petalis 13 cm. longis, plus minusve aurantiacis; columnis staminalibus 10–11 cm. longis, glabris; ovariis hispidis pilis urentibus 3–4 mm. longis.

TYPE: Panama, Veraguas, lower montane wet forest, 6–7 km. W. of Santa Fé on new road past agricultural school, alt. 2900 ft. [ca. 885 m.], tree 8 m. tall, 20 cm. d.b.h., area of older secondary growth, calyx turning red in fruit, petals orange at base, yellow-orange at tip, anthers yellow, stigmas velvety, deep red-purple, odorless, 17 Feb. 1974, *Nee 9842* (holotype, MO; isotypes, LL, US).

Tree to 8 meters tall; stems densely stellate-pubescent. Leaf blades to at least 20 cm. long, 24 cm. broad, cordate, weakly 5-angled or -lobulate, margin obscurely undulate-crenate, lobes subacute, palmately 9-nerved, upper surface with scattered stellate hairs, with radii tending to be antrorsely oriented and veins more densely pubescent, lower surface stellate-tomentose (densely so and whitish when young). Petioles shorter than blades, densely and uniformly stellate-pubescent like stem. Stipules 13–30 mm. long, 12–21 mm. broad, broadly rounded, obtuse to acute, densely stellate-pubescent, parallel veined. Pedicels at anthesis 13 cm. long, about equaling subtending petioles, with pubescence like that of stem. Involucel 5 cm. long, gamophyllous and spathaceous, minutely stellate-pubescent, irregularly toothed apically, deciduous. Calyx 3.5–6.5 cm. long, about 1/2- or less divided, minutely stellate-pubescent, "turning red in fruit"; lobes 3-nerved, 15–20 mm. long, 8–16 mm. broad at sinus, acute. Petals 13 cm. long, "orange at base, yellow-orange at tip," stellate-pubescent externally, glabrous internally. Staminal column 10–11 cm. long, glabrous, densely staminiferous in distal 2 cm.; filaments 3–5 mm. long. Style exceeding androecium and 5-parted apically; stigmas 5, purplish, capitate; ovary densely beset with antrorse, pungent hairs 3–4 mm. long. Fruits and seeds unknown.

DISTRIBUTION. Panama (MAP 2); known only from the type locality.

Wercklea grandiflora is distinctive for its long (5 cm.), spathaceous involucel

and perhaps for its more or less orange corolla. It shows certain similarities with *W. magnibracteata* (q.v.).

9. **Wercklea lutea** Rolfe, Kew Bull. **1921:** 118. 1921. TYPE: Costa Rica, San José, Las Nubes, on the slopes of Irazú, flowers clear lemon yellow, Feb. 1920, *Lankester s.n.* (holotype, K, photo MO; isotypes, K (2 sheets)). FIGURES 3, 25, 26.

Hibiscus rolfeanus A. Robyns, Ann. Missouri Bot. Gard. **52:** 177. 1965 (based on *Wercklea lutea* Rolfe). *Hibiscus luteus* (Rolfe) L. O. Williams & A. Robyns, Ann. Missouri Bot. Gard. **53:** 114. 1966.

Shrub or tree 3–10 meters tall; stems densely stellate-pubescent to glabrate, sometimes with scattered, conical prickles 3–5 mm. long. Leaf blades to at least 21 cm. long, 35 cm. wide, subcordate to cordate, orbicular to ovate, often weakly lobulate, prominently and remotely dentate to subentire, often acute, sometimes obtuse, palmately 7- to 9-nerved, discolorous, both surfaces sparsely and minutely stellate-pubescent, densely so on veins, rarely with few ligneous prickles on main veins beneath. Petioles $\frac{1}{2}$–$\frac{4}{5}$ length of blades, usually densely stellate-pubescent, rarely with few ligneous prickles. Stipules 8–22 mm. long, about as wide, broadly triangular-ovate to rotund, acute, stellate-pubescent, deciduous. Pedicels solitary in leaf axils, usually exceeding subtending petiole, 4–16 cm. long at anthesis to 21 cm. long in fruit, stout (5–6 mm. in diameter) and woody in fruit, sparsely to densely stellate-pubescent, more densely so at base of flower, sometimes with small (1–2 mm.), swollen-based, pungent hairs near base of flower. Involucel 2–3 cm. long, usually of 3 bracts; bracts more or less connate or splitting to base, ovate-sessile, 14–30 mm. wide, stellate-pubescent. Calyx 3.5–4.5(–5.5) cm. long, $\frac{1}{2}$- to $\frac{1}{3}$-divided, minutely stellate-pubescent, toward the base hispid and sometimes with swollen-based, pungent hairs 2 mm. long, the spinescent tips often bifurcate or stellate; lobes 3- to 5-nerved, triangular or ovate, acute, 12–22 mm. broad at sinus, minutely woolly internally especially along margin. Petals 8–13 cm. long, yellow, externally stellate-pubescent except toward base. Staminal column glabrous, staminiferous in distal 2 cm.; filaments 3–8 mm. long. Fruit a 5-angled or -winged capsule, 4–7 cm. long, obovoid, acuminate, beaked, externally densely hispid with hairs 2–3 mm. long, internally hispid along suture margin. Seeds 4 mm. long, reniform, blackish, with sparse, brownish, bristly hairs 1–2 mm. long.

DISTRIBUTION. Costa Rica (MAP 2), 1500–2500 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Cerros de Zurqui, NE. of San Isidro, wet forest, *Standley & Valerio 50429* (US); 12 km. NE. of San Rafael, *Wilbur et al. 15951* (DUKE); Yerba Buena, NE. of San Isidro, wet forest, *Standley & Valerio 49705* (US); between Río Las Vueltas and Río Nuevo (10°6′N., 84°3′W.), *Burger & Baker 9442* (F); Río Vueltas (upper Río Patria), eastern slope of Volcán Barba near Continental Divide (10°6′N., 84°4′W.), *Burger & Liesner 6412* (DUKE, F, MO); Las Vueltas region N. of Cerro Chompipe, ca. 15 km. NE. of Heredia and 3 km. N. of Cerro Redondo de la Cruz, *Utley & Utley 1307* (F). CARTAGO: riverside woods just above

dam under construction by I.C.E. in Project Tapantí, *Lent 2196* (F, MO (3 sheets)). SAN JOSÉ: 3–5 km. NE. of Cascajal in vic. of Río Cascajal, *Wilbur 24419* (DUKE); Volcán Barba, *Elias de la Sota 5078* (CTES, pf); Las Nubes, wet forest, *Standley 38702* (US), *Standley 38645* (US), *Standley 38339* (US), *Collado s.n.* (US).

Wercklea lutea is described as locally common in wet evergreen forests and along streams. It sometimes has a few prickles on the stems and leaves and is thus intermediate between the very prickly species (e.g., *W. ferox, W. horrida*) and those completely lacking prickles (e.g., *W. tulipiflora, W. insignis*). Additionally, this species has been noted to have "mucilaginous sap" (*Burger & Liesner 6412*) and a floral odor that is "slightly sweet" (*Webster et al. 12383*).

Wercklea lutea is characterized by its combination of yellow flowers, relatively long pedicels, and hispid fruits with prominent wings and beak. It differs from *W. woodsonii* specifically in the rounded form of the base of the involucel, as well as in the number and conformation of the individual divisions of the involucel. It may be unique in having often bifurcated or stellate pungent hairs at the base of the calyx.

10. **Wercklea woodsonii** (A. Robyns) Fryxell, comb. nov.

FIGURES 4, 5, 27, 28.

Hibiscus woodsonii A. Robyns, Ann. Missouri Bot. Gard. **52:** 179. *fig. 1.* 1965. TYPE: Panama, Chiriquí, vicinity of Bajo Chorro, alt. 1900 m., tree 20 m., fls. pale yellow, *Woodson & Schery 604* (holotype, US; isotype, MO).

Tree 4–20 meters tall; stems with minute, sparse to dense, stellate hairs, sometimes with "spiny trunk" (*D'Arcy & D'Arcy 6588, Lao 402*), or "spined when young" (*Heithaus 411*). Leaf blades to at least 24 cm. long, 30 cm. broad, cordate, indistinctly pentangular to suborbicular, remotely dentate to undulate, subacute to obtuse, palmately 7- to 9-nerved, discolorous, upper surface sparsely and minutely stellate-pubescent (densely so on veins), lower surface minutely stellate-pubescent. Petioles shorter than blades, 9–20 cm. long, with stellate pubescence like that of stem, more densely pubescent near juncture with blade. Stipules 12–30 mm. long, 10–20 mm. broad, triangular-ovate, acute, stellate-pubescent. Pedicels solitary or paired in leaf axils, at anthesis shorter than to somewhat longer than subtending petiole, 5–24 cm. long at anthesis to 16–31 cm. long and stout and woody in fruit (5–9 mm. in diameter), with pubescence like that of petioles (sparse proximally, dense distally). Involucel 1.5–3 cm. long, 8- or 9-parted, stellate-pubescent (densely so at base); bracts connate basally into cup with truncate base, lance-triangular to ovate-cordate, 4–12 mm. wide, margins more or less revolute basally, reflexed in fruit, persistent. Calyx 3–5 cm. long, ½- or less divided, densely and minutely stellate-pubescent throughout and with swollen-based pungent hairs 1–2 mm. long on tube; lobes prominently 3- to 5-nerved. Petals 8–13 cm. long, 5–6 cm. wide distally, yellow, stellate-pubescent externally except toward base. Fruit a prominently winged, woody capsule, fusiform

FIGURES 27–30. 27, 28, *Wercklea woodsonii:* 27, *D'Arcy & D'Arcy 6588,* in flower; 28, *Nee 9999* (see FIGURE 5), in fruit. 29, 30, *W. cocleana:* 29, *Dwyer 1918,* in flower; 30, *Gentry 5633,* in fruit.

to obovoid with gradually or abruptly acuminate beak, 5–7 cm. long including 1–1.5 cm. long beak, densely hispid externally with hairs 2–4 mm. long, sparsely pubescent internally on suture margin. Seeds 3.5 mm. long, reniform, blackish, sparsely pubescent with light brown, cottony to bristly hairs 1–2 mm. long.

DISTRIBUTION. Panama and Costa Rica (MAP 2), 1800–2700 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Panama.** CHIRIQUÍ: slopes of Cerro Punta, *Gentry 5860* (MO, US), *Lao 402* (MO); above Cerro Punta, frequent, *D'Arcy 5368* (MO); along road between Cerro Punta and Las Nubes, *Croat 26385* (MO, pf); slope of Cerro Respinga above town of Cerro Punta, frequent in thickets and forests, *D'Arcy & D'Arcy 6588* (F, LL, MO, NY); trail through Paseo de Respinga on way to Boquete, *Wilbur et al. 13184* (F); roadsides, pastures, and remnants of lower montane wet forests, Bajo Grande, 1–3 km. E. of town of Cerro Punta, *Nee 9999* (LL, MO, US); roadsides between Cerro Punta and Bajo Grande, *Croat & Porter 16008* (MO); disturbed cloud forest at Monte Rey, above Boquete, *Croat 15752* (MO); valley of Río Chiriquí Viejo, vic. of Monte Lirio, *White 41* (MO (3 sheets)); Río Chiriquí Viejo, near El Volcán, in open sunlight, wet habitat, *White 175* (F, MO). **Costa Rica.** SAN JOSÉ: ca. 25 km. N. of San Isidro de El General, along Interamerican Highway (9°29′N., 83°41′W.), in secondary scrub on steep slope, *Burger 8399* (DUKE, F, MO), *Williams et al. 28539* (BM, C, F); between La Georgiana and San Isidro, 2700 m. alt., *Stone 2040* (DUKE); 29 km. N. of San Isidro del General, *Wilbur 21113* (DUKE); Cerro de la Muerte, steep, wet, scrub-covered hillsides, ca. 3 mi. [4.8 km.] N. of Villa Mills, *Webster et al. 12383* (F, MO); Páramo, roadsides, steep slopes, *Heithaus 411* (MO); Cordillera de Talamanca, near La División, N. of San Isidro de El General, *Williams et al. 24383* (F); entre San Isidro del General y La División, *Jiménez 883* (F); ca. 10 mi. [16 km.] SE. of La Asunción, *Wilbur & Almeda 16965* (DUKE, F); entre Cerro de la Muerte y San Isidro del General, *Jiménez 277* (F), *Lems 5180* (F).

The flowers are described as "very fragrant" (*White 175*), and the calyces as "light green" (*White 175*), "slightly orange" (*D'Arcy & D'Arcy 6588*), or "reddish" (*D'Arcy 5368*).

Wercklea woodsonii is distinctive in the conformation of the involucel, which is characteristically truncate at the base, with the basal margins of the bracts more or less revolute. It may have a spinescent juvenile form (*Heithaus 411*), similar to that of *W. flavovirens*.

11. **Wercklea insignis** Pittier & Standley ex Standley, Contr. U. S. Natl. Herb. **18:** 112. 1916. TYPE: Costa Rica, San José, La Palma, *Wercklé s.n.* (holotype, US). FIGURES 6, 20.

Hibiscus wercklei A. Robyns, Ann. Missouri Bot. Gard. **52:** 178. 1965. Based on: *Wercklea insignis* Pittier & Standley ex Standley (non *Hibiscus insignis* Martius, 1876).

Tree 5–15 meters tall; older branches glabrate, with light tan bark. Leaf blades to at least 26 cm. long, 38 cm. wide, cordate, orbicular to flabelliform, obscurely dentate or subentire, obtuse or subacute, palmately 9- (to 13-)nerved,

upper surface sparsely stellate-pubescent to glabrate (remaining pubescent at juncture with petiole), lower surface sparsely stellate-pubescent. Petiole about equaling blades, sparsely stellate-pubescent to glabrate. Stipules 4–10 mm. long, 5–15 mm. broad, sessile, semicircular, obtuse or subacute, minutely and sparsely stellate-pubescent. Pedicels 1 to 3 in leaf axils, 1–10 cm. long at anthesis to 20 cm. long in fruit, sparsely stellate-pubescent to glabrate. Involucel 1.5–2.5 cm. long, gamophyllous, irregularly divided. Calyx 3–5(–6) cm. long, sometimes reddish, ca. 1/2-divided, minutely and very sparsely pubescent externally, glabrous internally except bearded on margins of lobes; lobes 3- to 5-nerved. Petals 10–15 cm. long, 5–6.5 cm. broad distally, lavender, ciliate on margin of claw, sparsely stellate-pubescent externally, glabrous internally except for minute, dark-pigmented, peglike vestiture especially near base. Staminal column 3–4.5 cm. long, pallid, subglabrous but with some peglike structures present; filaments 0.5–1 mm. long. Style slightly exceeding staminal column, glabrous, 5-parted for distal 1 mm.; stigmas 5, capitate, densely hairy, ca. 2 mm. in diameter. Fruit a winged capsule, obovoid, prominently beaked, 4.5–7 cm. long including 6–12(–18) mm. beak, densely hispid externally with hairs 3(–4) mm. long, glabrous internally. Seeds 3 mm. long, reniform, brownish, prominently pubescent, the hairs 3 mm. long, red-brown, cottony to bristly, patent.

DISTRIBUTION. Costa Rica (MAP 2), 750–1700 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Central de Montes de Oro, alt. 1200 m., "balsa-burío," *Lankester & Jiménez 1348* (F). ALAJUELA: *Lent 1183* (F, IJ, NY); El Silencio, *Smith P2124* (UC); between San Lorenzo and Los Angeles de San Ramón (10°14′N., 84°32′W.), *Burger & Antonio 11210* (F); near La Laguna, 6–8 km. S. of Villa Quesada, cut-over forest area in barranca, *Molina et al. 17503* (BM, DUKE, EAP, F, MO); near Zarcero, *Smith A708* (F); rain forest in gully, ca. 8 mi. [12.9 km.] S. of Quesada, *Webster et al. 12212* (MO); 12 km. N. of Balsa de San Ramón, *Utley & Utley 3753* (DUKE, F); Río Cataratas about 26 km. NNW. of San Ramón, *Wilbur et al. 22104* (DUKE). HEREDIA: waterfall of La Paz, Varablanca de Sarapiquí, *Stork 4671* (UC), *Burger & Burger 8006* (F), *Williams 20317* (F), *Lems 5020* (DUKE, F); dry fill area 8.1 km. N. of Vara Blanca on Hwy. 9, *Luteyn 609* (DUKE, MO); ca. 4.5 mi. [7.2 km.] N. of Vara Blanca, *Wilbur & Stone 10466* (DUKE, F); vic. of Angel Falls, slopes of Volcán Poas, *Godfrey 67307* (FSU, MO); frente a la catarata de El Angel, Río La Paz, entre San Miguel y Vara Blanca de Sarapiquí, *Jiménez 968* (F, NY); Lajas de Zapote, Alfaro Ruiz, *Jiménez 1807* (F). SAN JOSÉ: La Hondura, *Standley 37590* (US (2 sheets)), *Valerio 753* (F); vic. San José, cultivada en un jardin Guadalupe, *Jiménez 19* (US), *idem*, 1916, *Jiménez s.n.* (US), *Standley 33339* (US), *Popenoe 1022* (US); Sr. Jiménez garden, *Rowlee & Stork 286* (US); suburb of San José, *Rowlee & Stork 968* (US); below La Palma, *Burger 3892* (F, NY); La Palma, *Rowlee & Stork 254* (US); forêts de La Palma, *Tonduz 12536* (K, US (2 sheets)); La Palma area, NE. of San Jerónimo (10°2′N., 84°0′W.), *Burger & Antonio 11077* (F), *Burger & Visconti 10223* (F). CARTAGO: along Río Atirro ca. 2 km. E. of La Esperanza (9°47′N., 83°38′W.); elev. 850 m., *Taylor 18005* (NY); ca. 15 km. S. of Tapantí (9°42′N., 83°47′W.), *Burger & Liesner 6820* (F). Pejivalle, Riverside, *Lankester 878* (US (2 sheets)). Cascajal, *Lankester 329* (K (5 sheets), US).

Wercklea insignis is distinctive for its relatively sparse pubescence, subentire leaf margins, very short androecium (less than half the length of the petals), relatively small stipules, relatively long capsular beak, and prominently pubescent seeds. According to St. John (1973, p. 232), it has been introduced into cultivation in Hawaii.

12. **Wercklea cocleana** (A. Robyns) Fryxell, comb. nov. FIGURES 29, 30.

Hibiscus cocleanus A. Robyns, Ann. Missouri Bot. Gard. **52:** 176. 1965.

TYPE: Panama, Coclé, El Valle, shrub 25 ft. [7.6 m.] tall, fls. rose-red, 7 Dec. 1962, *Dwyer 1918* (holotype, MO-1802085; isotypes, BR, MO-1802086).

Tree 5–12 meters tall; twigs densely stellate-pubescent. Leaf blades to at least 20 cm. long, 24 cm. wide, cordate, orbicular, dentate, acute to obtuse, palmately 9- to 11-nerved, upper surface sparsely stellate-pubescent (densely so on nerves), lower surface densely stellate-pubescent. Petioles shorter than to longer than blades, densely to sparsely stellate-pubescent. Stipules not seen. Pedicels solitary in leaf axils, exceeding subtending petiole, 13–26 cm. long at anthesis to 30 cm. long in fruit, densely stellate-pubescent and sometimes also prickly. Involucel 1.5–3 cm. long, more or less gamophyllous, stellate-pubescent, deciduous, irregularly lobed, lobes triangular. Calyx 3–5.5 cm. long, ca. ½-divided, minutely stellate-pubescent and hispid with pungent hairs 1–2 mm. long especially toward base; lobes 3- to 5-nerved, ovate, acute, 10–16 mm. broad at sinus. Petals 7.5–12 cm. long, rose-red, stellate-pubescent externally except toward base. Staminal column 8–10 cm. long, stellate-pubescent (nearly glabrous apically), densely staminiferous in distal 2.5 cm.; filaments 3–5 mm. long. Fruit a winged capsule, obovoid, beaked, 5–6.5 cm. long including 5–8 mm. long beak, ca. 4 cm. broad, densely hispid, hairs 2 mm. long. Seeds "hairy."

DISTRIBUTION. Panama (MAP 2), 700–900 m. alt.

ADDITIONAL SPECIMENS EXAMINED. **Panama.** COCLÉ: La Mesa, *Gentry 5633* (F, MO); ca. 4 km. from El Valle near La Mesa, *Correa & Dressler 1001* (DUKE); near La Mesa, *Wilbur & Luteyn 11730* (DUKE); Valle de Antón, *Buitrago 42* (MO); between Cerro Pilón and El Valle de Antón, cloud forest, *Duke & Dwyer 13934* (GH, K, MO, UC, US (2 sheets)).

Wercklea cocleana is characterized by its combination of rose- or lavender-colored flowers, pubescent staminal column, very long pedicels, and prominently winged and beaked capsules.

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FRUITS AND SEEDS OF THE BRANDON LIGNITE, VI. MICRODIPTERA (LYTHRACEAE)

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THE BRANDON LIGNITE is a small deposit of brown coal and associated sediments of presumed Oligocene age in Forestdale, Vermont (lat. 43°50′ N., long. 73°03′ W.). It contains a rich flora and has been the focus of much research, including the present investigation of fruits and seeds. For a review of the history and geology of the site, see Tiffney (1977, 1979, 1980a) and Tiffney and Barghoorn (1976, 1979).

The specimens are compactions—three dimensional and retaining much of their original organic matter. They were recovered by disaggregating the matrix in either sodium carbonate or dilute hydrogen peroxide and sieving the resulting sediment for the small organic fraction. This was examined under a dissecting microscope, and the seeds were picked out with a fine brush. Specimens were stored in a 1 : 1 solution of glycerine and 50 percent alcohol. Sectioned material was embedded in paraffin by standard methods and cut at 10 μm. intervals. Whole specimens were photographed with a Nikon SMZ-10 dissecting microscope with a Nikon PFM photographic attachment; sectioned material with a Leitz Ortholux compound microscope equipped with the same photographic attachment. Scanning electron micrographs were made with a Perkin-Elmer ETEC U-1 Autoscan. Modern material of *Decodon* was obtained from herbarium specimens in the Gray (GH) and Arnold Arboretum (A) Herbaria of Harvard University.

GENERAL SURVEY OF THE FOSSIL FRUITS AND SEEDS OF THE LYTHRACEAE

The Lythraceae is a cosmopolitan, predominantly tropical family of 22 to 25 genera and 450 to 550 species of herbs, shrubs, and trees (Engler, 1964; Willis, 1973; Heywood, 1978). Many of the herbs are aquatics, and other members of the family commonly inhabit damp ground (Graham, 1964). The shrubs and trees include both evergreen and deciduous members. The family is well represented in the fossil record by fruits and seeds. General reviews of the fossil history of the group have been provided by Sahni (1943), Graham and Graham (1971), and Eyde (1972). Two tribes are recognized in the modern family, based on the completeness of septation of the capsule (Koehne, 1903; Engler, 1964): in the Lythreae septation is not complete to the apex, while in the Nesaeeae it is. This character, however, is often difficult to apply (Graham, 1964).

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Many of the fossils cannot be ascribed to one section or the other because they are too poorly preserved. These include *Cranmeria trilocularis* Reid & Chandler (Chandler, 1961a), *Pachyspermum quinqueloculare* Reid & Chandler (Reid & Chandler, 1933), *Tamesicarpum polyspermum* Reid & Chandler (Chandler, 1961a), all from the latest Paleocene and Early Eocene of southern England, and *Enigmocarpon parijai* Sahni (Sahni, 1943) from the Paleogene Deccan Intertrappean series of India.

Ammannia lakensis Chandler (Chandler, 1962), from the Lower Eocene of southern England, is the oldest known representative of the Lythreae. *Palaeolythrum bournense* Chandler has been reported from Middle Eocene sediments in southern England, and *P. gailense* Chandler from the Pliocene of France (Chandler, 1963b). *Lythrum* L. is known from the Japanese Pliocene (Miki, 1959).

Nesaeeae are also first recognized in the Early (*Alatospermum lakense* Chandler; Chandler, 1962) and Middle (*Ministerocarpum alatum* Reid & Chandler; Reid & Chandler, 1933) Eocene of southern England, and *Lagerstroemia indica* L. is known from the Pliocene of Japan (Miki, 1937). Mai (1960, 1964) reported two species of *Lagerstroemia*, *L. lignitum* (Menzel) Mai and *L. europaea* Mai, from Miocene sediments in Germany. Subsequent investigation resulted in the transfer of both species to *Polyspora* Sweet (= *Gordonia* Ellis; Theaceae) (Mai, 1971; Gregor, 1978a, 1978b). The seeds of *Decodon* J. F. Gmelin, *Microdiptera* Chandler, and *Mneme* Eyde, together with those of *Alatospermum*, comprise a morphological complex to which the Brandon fossils belong. This necessitates a review of the systematic history, morphological characters, and geologic distribution of these genera in order to place the Brandon specimens in context.

FOSSIL RECORD OF DECODON AND RELATED TAXA

C. and E. M. Reid (1907) illustrated (but did not describe) an unidentified seed from the Pliocene of Tegelen, The Netherlands. This seed was subsequently reported from Raevels, Belgium (C. & E. M. Reid, 1908), and from Reuver, The Netherlands (C. & E. M. Reid, 1915), both of Pliocene age. In the last publication, the fossil was compared to *Stocksia* Bentham (Sapindaceae). A closely allied species was then found from the Pliocene of France. In 1920 E. M. Reid indicated that these specimens could not be compared to *Stocksia* and then proposed *Diclidocarya*, in which she included *D. gibbosa* (E. M. Reid, 1920) and *D. globosa* (E. M. Reid, 1923), from Pliocene sediments of western Europe and Russia, and *D. menzelii* (E. M. Reid, 1927), from the Oligocene of Germany. The familial affinities of the genus were regarded as uncertain, although the species were considered to be aquatics (E. M. Reid, 1920).

P. A. Nikitin (1929) recognized that the morphology of these seeds matched that of the extant monotypic *Decodon* of eastern North America and transferred *Diclidocarya globosa* to *Decodon globosus* (E. M. Reid) P. A. Nikitin. E. M. Reid (1929), in an article appended to Nikitin's, agreed to this identification and extended it to include the type species of *Diclidocarya*, *D. gibbosa*, which became *Decodon gibbosus* (E. M. Reid) E. M. Reid. However, Reid's

analysis indicated that *Diclidocarya menzelii* was distinct from *Decodon* at the generic level, and she retained *D. menzelii* without providing a new generic name in place of *Diclidocarya,* now a synonym of *Decodon.* Eyde (1972) resolved this problem by providing the name *Mneme.* Chandler (1957) established a third genus of related fossil seeds, *Microdiptera* Chandler.

Decodon. Thirteen species of *Decodon* are presently recognized (*D. tetraedriformis* Raniecka-Bobrowska (Raniecka-Bobrowska, 1957) has been recognized as a synonym of *D. globosus* (Dorofeev, 1963a; Friis, 1980)). The majority of these species, as well as most of the individual reports, are from Siberia, but the genus was also widespread in western Europe. The number of species was low in the Eocene (one), increased in the Oligocene (five), peaked in the Miocene (ten), and shrank in the Pliocene (four), leading to the single extant species. The genus is of sufficient interest to have warranted reviews by Raniecka-Bobrowska (1957) and Dorofeev (1977a), the latter including the description of nine new species from the U.S.S.R. Two incomplete maps of fossil distributions have been published (Dorofeev, 1963c; Palamarev, 1970). A reasonably complete enumeration of the reported fossils is given in TABLE 1.

The seeds of *Decodon* are anatropous and bitegmic and are borne about 20 to 30 per 3- or 4-loculed capsule of approximately 5–6 mm. diameter. Because the seeds are tightly packed within the fruit, they are generally elongate-pyramidal (PLATE I, A, C), with sharply rounded or angular corners and no clear lateral wings. There is a wide variation in shape due to degree of locular compression and stage of development. The seeds vary between 0.8 and 1.9 mm. in length (average, 1.2 mm.) and 0.6 and 1.9 mm. in width/thickness (average, 0.98 mm.). The raphe commences at the apical point beneath the micropyle and runs through the dorsal[1] face to the base

[1]There is some confusion in distinguishing the dorsal and ventral faces. E. M. Reid (1920; also 1927, 1929), in establishing *Diclidocarya* (= *Mneme*), considered the germination valve to be on the ventral face and the raphal crest to be on the dorsal. This usage has been followed by many subsequent authors (e.g., Kirchheimer, 1957; Mai & Walther, 1978; Friis, 1980) in descriptions of *Decodon*, *Mneme,* and *Microdiptera*. Chandler followed this convention in describing *Decodon gibbosus* (1960) and *D. vectensis* Chandler (Chandler, 1963a). However, in describing *Microdiptera parva* Chandler (Chandler, 1957, 1961b, 1963a), *Mneme minor* Chandler (Chandler, 1960), and *Alatospermum lakense* Chandler (Chandler, 1963b), she considered the germination valve to be on the dorsal face, a distinction also followed by Mai (1964) for *Microdiptera parva* and Holý (1976) for *Mneme donata*.

The question of correct interpretation can be determined only from the relationship of the seeds to the fruit axis. Fossil fruits are known in two cases. That reported by Holý (1976) is not described in detail. In *Microdiptera major* Chandler (Chandler, 1963b) the seeds are packed in tightly overlapping longitudinal rows, with their flat faces parallel to the long axis of the fruit, the individual seeds radiating in a "starburst" from the central columella. The same relationship is seen in the fruits of modern *Decodon*. As a result, a logical distinction between dorsal and ventral faces cannot be made, and a choice between the two becomes arbitrary. Indeed, the distinction is perhaps completely unwarranted, but its use is so entrenched in the literature that its rejection would confuse, rather than clarify, matters. This paper follows E. M. Reid's original usage in treating the germination valve as ventral and the raphe as dorsal. Discovery of new fossil fruits may modify this conclusion.

TABLE 1. **Reported Taxa of Decodon.**

Taxon	Age	Locality	Citation
Sect. GIBBOSUS Dorofeev			
Decodon gibbosus (E. M. Reid) E. M. Reid			
f. *gibbosus*, f. *elongatus* Dorofeev	Late Eocene	Barton Beds, England	Chandler, 1960
	Oligocene?	Svetlogorsk, Lithuania	Dorofeev, 1963b
	Oligocene	W. Siberia, USSR (9 localities)	Dorofeev, 1963a
	Oligocene	Tara, W. Siberia, USSR	Dorofeev, 1957a
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	Rostov, Ukraine, USSR	Dorofeev, 1959b
	Miocene	W. Siberia, USSR (9 localities)	Dorofeev, 1963a
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
	Miocene?	Bashkiria, S. Urals, USSR	Kolesnikova, 1960
	Mid Miocene	Fasterholt, Denmark	Friis, 1980
	Mid/Late Miocene	Irtysh R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1951
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1955b, 1955e
	Late Miocene	NE. Moldavia, USSR	Negru, 1972
	Late Miocene	SW. Moldavia, USSR (6 localities)	Negru, 1979
	Pliocene	Bug R., Tiligul R., W. Siberia, USSR	Dorofeev, 1955d

	Pliocene	Pont de Gail, France	E. M. Reid, 1920
Sect. Globosus Dorofeev			
D. aldanensis Dorofeev	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1977a
D. bashkiricus Dorofeev	Pliocene	Bashkiria, S. Ural Mts., USSR	Dorofeev, 1977a
D. europaeus Dorofeev	Miocene	Tambov region, Russia, USSR	Dorofeev, 1977a
D. globosus (E. M. Reid) P. A. Nikitin	Oligocene	Tara, W. Siberia, USSR	Dorofeev, 1957a
	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
	Miocene	Rostov, Ukraine, USSR	Dorofeev, 1959b
	Miocene	W. Siberia, USSR (6 localities)	Dorofeev, 1963a
	Miocene	Stare Gliwice, Poland	Szafer, 1961
	Mid/Late Miocene	Irtysh R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	NE. Moldavia, USSR	Negru, 1972
	Late Miocene	Vienna Basin, Austria	Knobloch, 1976a
	Late Miocene	Bug R., Tiligul R., W. Siberia, USSR	Dorofeev, 1955d
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1955b, 1955e
	Late Miocene	Konin, central Poland	Raniecka-Bobrowska, 1959
	Late Miocene	SW. Moldavia, USSR (5 localities)	Negru, 1979
	Miocene/Pliocene	Domajski Wierch, Poland	Szafer, 1952
	Pliocene	Tegelen, Netherlands	E. M. Reid, 1927
	Pliocene	Raevels, Belgium	E. M. Reid, 1927
	Pliocene	Reuver, Netherlands	E. M. Reid, 1927
	Pliocene	Bashkiria, Russia, USSR	Dorofeev, 1960

TABLE 1 (*continued*).

Taxon	Age	Locality	Citation
D. globosus (E. M. Reid) P. A. Nikitin (cont'd.)	Pliocene	Bashkiria, Russia, USSR	Dorofeev, 1977b
	Pliocene	Kama R., Ural Mts., USSR	Dorofeev, 1957b
	Pliocene	Matanov Garden, S. Russia, USSR	Dorofeev, 1966
	Pliocene	Baldevo, SW. Bulgaria	Palamarev, 1970
	Pliocene	Pont de Gail, France	Reid, 1923
D. maeoticus Dorofeev	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1977a
D. nikitinii Dorofeev	Miocene	Lezhanka, W. Siberia, USSR	Dorofeev, 1977a
D. sibiricus Dorofeev	Oligocene	W. Siberia, USSR (4 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Early/Mid Miocene	Polevskoi, Ural Mts., USSR	Dorofeev, 1970
	Miocene	W. Siberia, USSR (7 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
D. sphenosus G. Bal.	Unknown	W. Siberia, USSR	V. P. Nikitin, 1968
D. tanaiticus Dorofeev	Pliocene	Krivobor'e, Ukraine, USSR	Dorofeev, 1977a
Sect. VECTENSIS Dorofeev			
D. antiquus Dorofeev	Miocene	Tambor region, Ural Mts., USSR	Dorofeev, 1977a
D. tavdensis Dorofeev	Oligocene	Sverdlovsk region, Ural Mts., USSR	Dorofeev, 1977a
	Mid Miocene	Fasterholt, Denmark	Friis, 1980
D. vectensis Chandler	Oligocene	Isle of Wight, England	Chandler, 1963a
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Mid Miocene	Fasterholt, Denmark	Friis, 1980

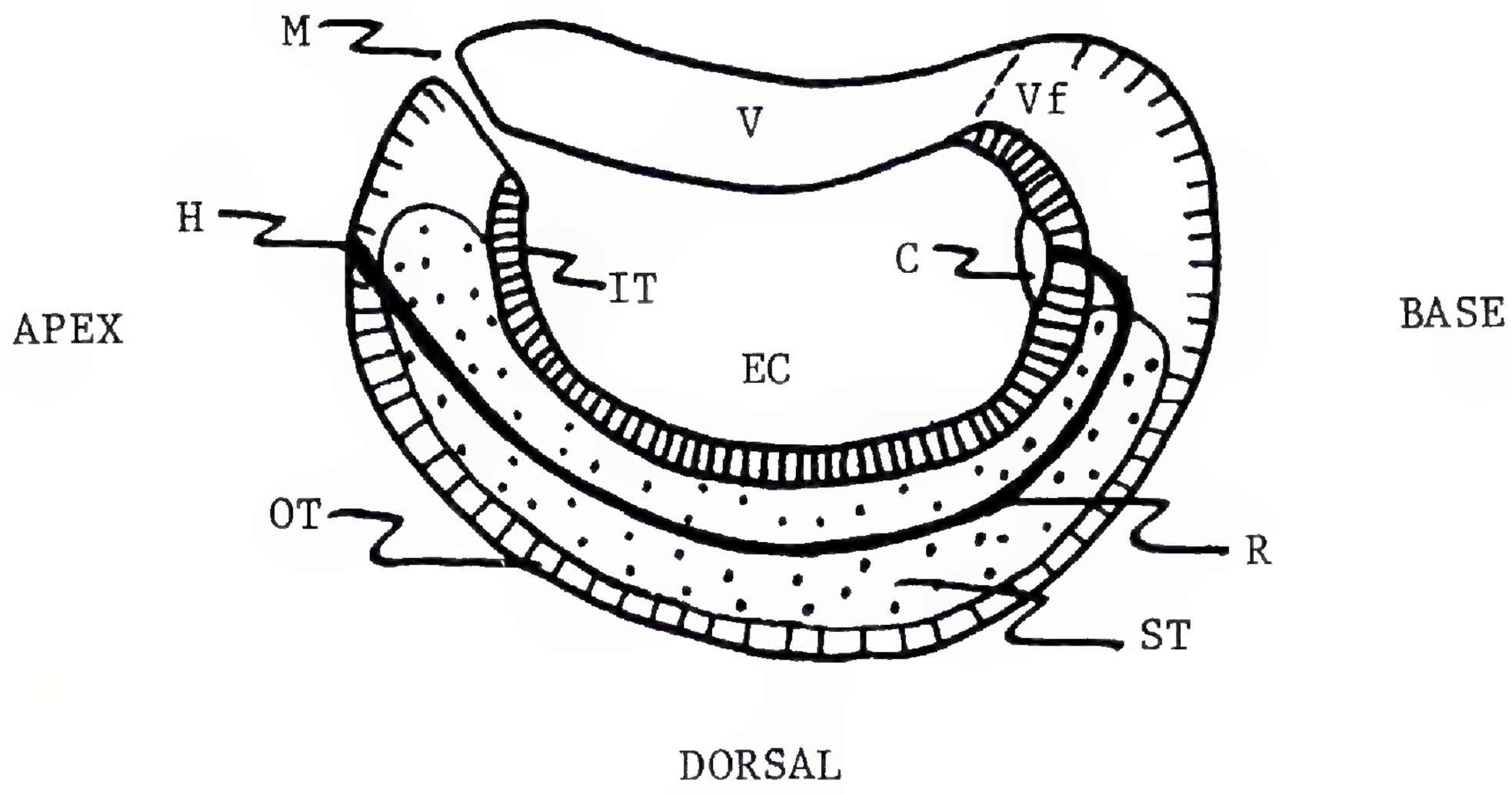

FIGURE 1. *Decodon verticillatus*, longitudinal section (after P. A. Nikitin, 1929). V = valve, Vf = valve flexure, C = chalaza, IT = crystal-bearing inner testa, EC = embryo cavity, R = raphe, ST = spongy tissue, OT = outer testa, H = hilum, M = micropyle.

of the seed, where it enters the obovoid embryo cavity via the expanded chalaza (see FIGURE 1; PLATE I, B). There are no furrows on the dorsal face. The oblong, slightly concave germination valve occupies one half to three quarters of the width of the ventral face, and one half to three quarters of its length (PLATE I, A). The surface of the valve is marked by six to twelve longitudinal rows of small pits that are 30–40 μm. in diameter. In modern seeds this detail is largely obscured by the thick epidermal coat. At maturity, the valve separates from the central body along its apical and lateral margins, pivoting on its attached base, and thus exposes the ellipsoid embryo cavity. The micropyle is situated at the apex of the seed, between the tip of the germination valve and the hilar scar (PLATE I, B). The structure of the outer integument is complicated (PLATE III, D). The outermost stratum is 14–52 μm. thick and is formed of one or two layers of large, elongate to equidimensional (14–36 × 21–52 μm.) epidermal cells with dark contents. This expands to eight to ten cells in thickness over the concave germination valve, making the seed surface in this area appear flat or slightly convex. There is some tendency for the epidermis to thicken over the two basal corners of the seed. Beneath the epidermis is an attenuated (15–21 μm.) outer sclerotesta of one or two equiaxial to elongate sclereids, 10–18 × 18–30 μm. in size; this layer thickens beneath the germination valve and there becomes contiguous with the inner sclerotestal wall surrounding the embryo cavity. The inner sclerotesta is approximately 45–75 μm. thick and consists of five to seven layers of irregularly shaped, small (17–41 μm.), thick-walled

cells that frequently contain octahedral crystals in their lumina. Where the outer testa abuts the germination valve, the delimiting cells become palisadelike and function as the zone of weakness along which the valve opens (P. A. Nikitin, 1929; see PLATE II, C, D for a similar structure in *Microdiptera*). Between the outer and inner sclerotestae on the dorsal and (to some degree) lateral faces is an intermediate layer of isodiametric spongy parenchyma cells 12–33 μm. in diameter, which presumably aid in flotation dispersal of the seed. When seen three dimensionally, this tissue forms a bowl that cups the embryo cavity and has a dip in its margin beneath the germination valve. The raphe occupies a tunnel curving through this spongy layer from apex to base (FIGURE 1; PLATE III, D). The inner integument is formed of a single layer of elongate (9–18 × 50–105 μm.) cells sheathing the embryo cavity.

Dorofeev (1977a; see also Friis, 1980) recognizes three morphological species groups in *Decodon*. The gibbosus group includes one species, *D. gibbosus* (33 reports), which ranges from Late Eocene to Pliocene. The seeds have narrow ventral faces, rounded edges, and well-developed dorsal tissue (FIGURE 2, a). Dorofeev (1955e) further divided this group into two forms: f. *gibbosus*, characterized by wedge-shaped seeds with moderately developed dorsal spongy tissue; and f. *elongatus*, in which the dorsal spongy tissue is strongly developed. No published report exists of the relative thicknesses of the internal and external sclerotestal walls of the dorsal face in the gibbosus group. The globosus group includes *D. aldanensis* Dorofeev, *D. bashkiricus* Dorofeev, *D. europaeus* Dorofeev, *D. globosus* (E. M. Reid) P. A. Nikitin, *D. maeoticus* Dorofeev, *D. nikitinii* Dorofeev, *D. sibiricus* Dorofeev, *D. tanaiticus* Dorofeev, and the living species *D. verticillatus* (L.) Ell. (48 reports) and ranges from the Oligocene to the present. One further member of the

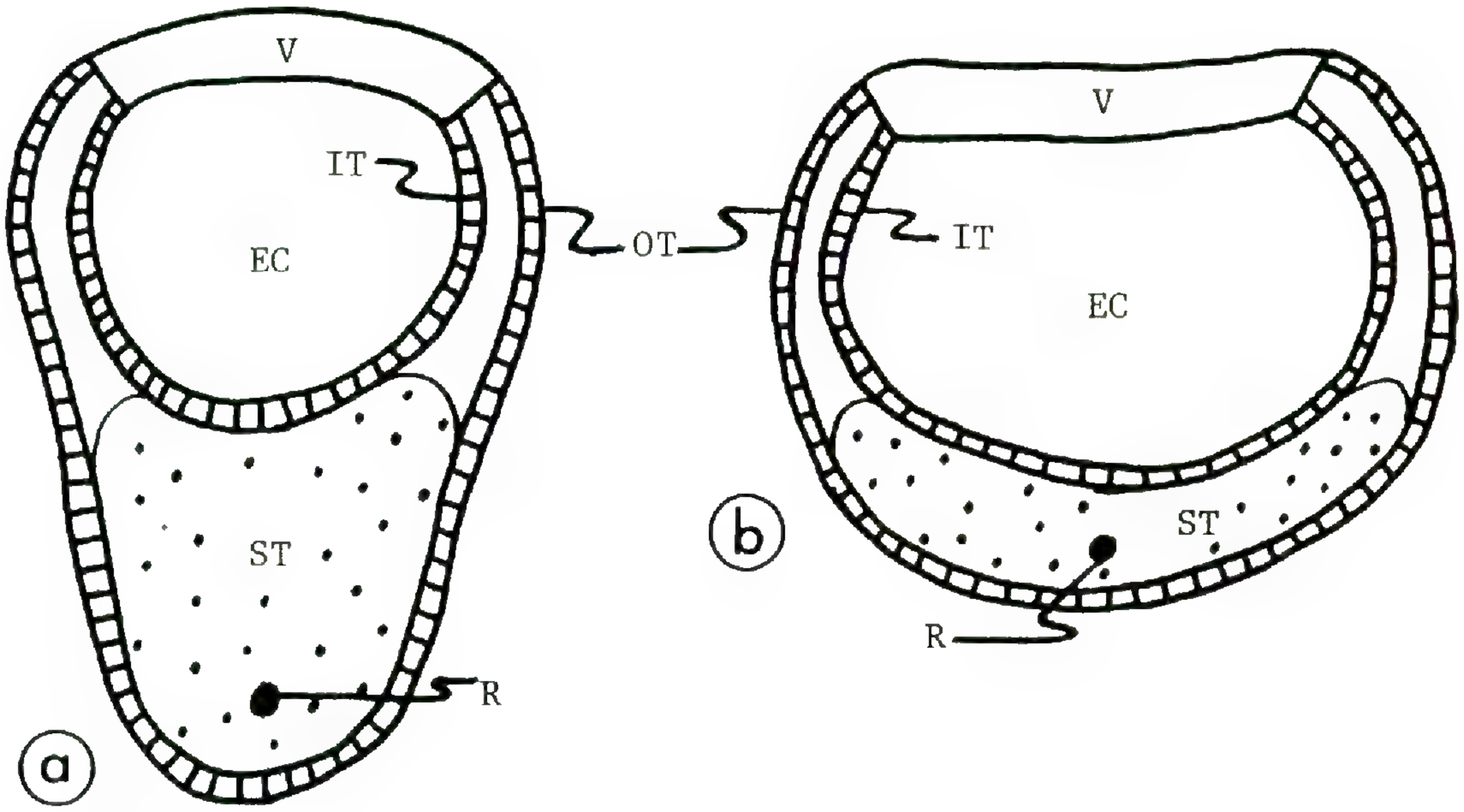

FIGURE 2. Cross sections: a, *Decodon gibbosus;* b, *D. globosus*. Conventions as in Figure 1.

group, *D. sphenosus* G. Bal., is potentially unique morphologically; however, this name is a *nomen nudum* since it was not validly published. Seeds of the globosus group have broad ventral faces, rounded edges, poorly developed dorsal spongy tissue (FIGURE 2, b), and a germination valve extending almost the full length of the ventral face. P. A. Nikitin (1929) noted that the lateral margins of *D. globosus* are convex to straight and that the external sclerotesta of the dorsal face is thicker than the inner, in contrast to *D. verticillatus*, which has straight to concave lateral margins and a thin external and thick internal sclerotesta. The vectensis group includes *D. antiquus* Dorofeev, *D. tavdensis* Dorofeev, and *D. vectensis* Chandler (six reports), ranging from Oligocene to Middle Miocene. Seeds of this group are characterized by a narrow ventral face, sharply angled edges, weak development of the dorsal spongy tissue, and a germination valve that extends most of the length of the ventral face. In *D. vectensis* the inner dorsal sclerotestal wall is thicker than the outer (Chandler, 1963a).

The only absolute character of apparent value in *Decodon* is the thickness of the inner and outer sclerotestae, although data on this are limited. In *D. verticillatus* and *D. vectensis* the outer testa is thinner than the inner, while in *D. globosus* the outer is thicker than the inner. This author is not aware that the character has been reported for other species. Beyond this, species delimitation is based on size and shape—both characters of continuous variation. None of the size distinctions between species is supported by statistical analysis, and the narrow range of seed size (0.5–1.9 mm.) in the genus, together with the complete overlap of species size ranges, suggests that the character is of little value, an opinion already expressed by Chandler (1960). Shape is little better. Some of the more elongate forms (e.g., *D. tavdensis, D. antiquus*) are distinctive, but these overlap in morphology both with each other and with more angular specimens of other species. *Decodon gibbosus* and *D. globosus* are classically separated by the greater development of dorsal spongy tissue in the former (FIGURE 2), but this also may simply be a gradational feature of no taxonomic importance. Mai (Mai *et al.*, 1963) suggested that *D. gibbosus* and *D. globosus* were but extremes of a continuum and subsequently (Mai & Walther, 1978) reduced the two to one species, *D. gibbosus*, with two subsidiary groups corresponding to *D. gibbosus* and *D. globosus*. He further suggested that the species of Dorofeev (1977a) were but forms within these groups. In the absence of an examination of all the fossil forms, this cannot be conclusively proved, but the present author is in full agreement with Mai's opinion.

Mneme. The seeds of *Mneme* are anatropous and bitegmic. At least in *M. menzelii* (E. M. Reid) Eyde, the 30 to 40 seeds were borne in a 4- to 6-locular capsule (Kirchheimer, 1957). The seeds are generally flattened and subcircular to oval in face view, with the ventral surface convex and the dorsal flat to convex. The central embryo cavity is normally flanked by two clear "wings," although these are nearly absent in some species of *M. sibirica* (P. A. Nikitin) Eyde, which is quite variable in shape. In a specimen of *M. menzelii* from Frecheu, West Germany, studied and illustrated here (PLATE III, A, B),

the wings are particularly clear, perhaps partly due to compression. The relative lack of variability in published specimens of *M. menzelii*, in contrast to those of *M. sibirica*, may involve the degree of packing of seeds in the capsule. The seeds of *Mneme* generally range from 1 to 2.5 mm. (average, 1.5 mm.) in length, and from 1 to 2.4 mm. (average, 1.4 mm.) in width. *Mneme minor* (Chandler) Eyde has much smaller (0.75–0.85 × 0.8–0.95 mm.) seeds. The raphe runs from the apical hilum along the dorsal testa to the basal chalaza; the lateral localization of spongy tissue dictates that the raphe is nearer the seed surface than in *Decodon*. The path of the raphe is generally flanked by two deep, narrow depressions (Friis, 1980; FIGURE 4, a), which extend about three quarters of the length of the seed and separate the wings from the body. These are nearly absent in *M. donata* Holý (Holý, 1976). Friis (1980) indicates that the central body is fully embedded in the wing tissue in *Mneme*. The elongate-elliptic germination valve fills one quarter to one third the width and one half to two thirds the length of the ventral face, although in *M. sibirica* it can occupy one sixth to four fifths the width due to overall variability in seed shape. In the specimen of *M. menzelii* from Frecheu (PLATE III, A) and in specimens examined by Friis (1980), the surface of the cap is lined by approximately twenty parallel rows of small pits. However, in seeds of this species illustrated by Knobloch (1976b, *pl. 1, fig. 18*) and in drawings of this species provided by Dorofeev (1969, *fig. 35*), six to nine rows of pits seem to be present. In *M. donata* the valve has eight rows of pits. The valve detaches completely from the testa to reveal the ellipsoid embryo cavity, which runs the full length of the seed. The micropyle is ventral to the hilum on the apical terminus, just beneath the termination of the valve. The seed is surrounded by a thick, dark epidermal layer (E. M. Reid, 1927). The outer integument forms a strong testa of radially elongate sclereids around the seed body but is differentiated into three layers on the lateral wings. Here an intermediate layer of spongy, isodiametric, 6–12 μm. cells with pitted walls (Friis, 1980) is developed. This is bounded to the exterior by a 35–45 μm. thick outer sclerotesta (measurements from Frecheu specimen) and to the interior by the lateral walls of the "inner" sclerotesta around the seed body. In specimens of *M. menzelii* from Senftenberg (E. M. Reid, 1927) the outer sclerotesta is thinner than the inner. The outer and inner sclerotestae unite on the ventral and dorsal surfaces of the central body. The sclerotesta thins beneath the germination valve, where it is apparently rich in crystalline inclusions in the cell lumina (Friis, 1980). The inner integument is formed of thin cells 50–60 μm. long and 6 μm. wide. This summary is based on published material and on a specimen of *M. menzelii* from Frecheu, West Germany, that is now in the Paleobotanical Collections of the Botanical Museum, Harvard University (#51392).

With the exception of two reports (*Mneme* sp. (Dorofeev, 1963a, 1969) and *M. triangulata* G. Bal. (V. P. Nikitin, 1968; possibly a *nomen nudum*)) for which full information is not available, there are three species. *Mneme menzelii* (27 reports) is the most common, ranging from (?Oligocene) Miocene to Pliocene and from Siberia to west-central Europe. It is primarily distinguished by the moderate to strong development of the lateral wings, and

by the indistinct separation of the wings from the central body. The latter feature may be a function of the inflated nature of the wings (FIGURE 4, a). *Mneme sibirica* is known from eight localities of Oligocene to Miocene age in western Siberia. It is highly variable in morphology (e.g., P. A. Nikitin, 1965, *pl. 14, figs.* 1–3) and is separated only with difficulty from *M. menzelii*. *Mneme minor* is the oldest; it is known from one report from the Late Eocene of southern England. It is distinguished by its small size and by the clear separation between the wing and the body. *Mneme donata* was described by Holý from Miocene sediments in Czechoslovakia. Its characters are closer to those of *Microdiptera,* to which it is here transferred. A summary of published reports is given in TABLE 2.

Microdiptera. The seeds of *Microdiptera* are generally similar to those of *Mneme.* They are anatropous and bitegmic and were borne in a multilocular, presumably capsular, fruit (Chandler, 1963b). The seeds tend to be dorsiventrally flattened, with the ventral surface convex and the dorsal concave to flat. The shape is irregularly obtriangular, varying from small and elongate to larger and broader forms. The corners are generally rounded but may be sharply angled in *M. major* Chandler and *M. uralensis* (Dorofeev) Friis. (The latter name is here used in a provisional sense—it is a *nomen nudum* since it has not been formally published.) Although the lateral wings are generally large and flat, they are sometimes narrow (e.g., *M. elongata* (Dorofeev) Dorofeev, *M. uralensis*, and some specimens of *M. parva* Chandler). The seeds range from 0.9 to 2 mm. (average, 1.25 mm.) in length, and 0.5 to 2 mm. (average, 1.26 mm.) in width. The path of the raphe follows the dorsal side of the seed body as in *Mneme*, and it is flanked by two depressions that extend nearly the full length of the seed and separate the wings from the seed body (PLATE II, F; FIGURE 3, b). Friis (1980) suggests that these grooves are shallow (FIGURE 4, b), although in some illustrated specimens of *M. parva* (e.g., Chandler, 1963a), *M. major* (Chandler, 1963b, *pl. 19, figs. 9, 13*), *M. uralensis* (Dorofeev, 1970, *fig. 12*), and the Brandon specimens (PLATE II, F) they appear to be deep. Friis (1980) describes the central body as being only partially embedded in the wing tissue, protruding about half of its diameter above the ventral face of the wing (FIGURE 4, b). The convex, oval to elliptic germination valve occupies between one quarter and one half the width of the ventral face (PLATES I, D–F; II, A, B) and about half its length, although in one report of *M. parva* (Chandler, 1963a) it reaches about four fifths the length. The surface of the valve is traversed by five to eight (rarely to ten) longitudinal rows of equiaxial pits about 40–50 μm. in diameter (PLATE II, B). At maturity the valve falls off completely to expose the ellipsoid embryo cavity that stretches the full length of the seed. The micropyle is just beneath the apical terminus of the germination valve, ventral to the hilum. Only small remnants of the apparently thick cuticle have been observed (PLATE III, E, F), beneath which can be seen a thin layer of narrow (5–7 μm.), elongate (50–60 μm.) cells (PLATE II, C, E) that are particularly noticeable around the germination valve (Chandler, 1957, 1961b). The outer integument forms a lignified testa two or three cells

TABLE 2. **Reported species of Mneme.**

Species	Age	Locality	Citation
Mneme donata Holý	See *Microdiptera donata* (Holý) Tiffney		
M. menzelii (E. M. Reid) Eyde	Oligocene?	Novonikol'skogo, W. Siberia, USSR	Dorofeev, 1955a
	Miocene	Senftenberg, E. Germany	E. M. Reid, 1927; Kirchheimer, 1935, 1957
	Miocene	W. Siberia, USSR (5 localities)	Dorofeev, 1963a
	Miocene	Rostov region, USSR	Dorofeev, 1959b
	Miocene	Fasterholt, Denmark	Friis, 1980
	Miocene	Yakutsk, Siberia, USSR	Dorofeev, 1969
	Miocene	Rypin, Poland	Łańcucka-Środoniowa, 1957
	Miocene	S. Poland	Łańcucka-Środoniowa, 1963
	Miocene	Tomsk, Siberia, USSR	P. A. Nikitin, 1935
	Miocene?	Bashkiria, S. Ural Mts., USSR	Kolesnikova, 1960
	Mid Miocene	Wiesa bei Kamenz, E. Germany	Mai, 1964
	Mid Miocene	Lausitz, E. Germany	Mai, 1967
	Mid/Late Miocene	Irtysh R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	Vienna Basin, Czechoslovakia	Knobloch, 1976a

	Late Miocene	S. Poland	Szafer, 1952
	Late Miocene	Konin, central Poland	Raniecka-Bobrowska, 1959
	Late Miocene	Kunovice, Moravia, Czechoslovakia	Knobloch, 1976b
	Late Miocene	Vienna Basin, Czechoslovakia	Čtyroký & Knobloch, 1976
	Miocene/Pliocene	Bol'shoĭ Yuksy, W. Siberia, USSR	Dorofeev, 1955c
	Pliocene	Razlog and Baldevo, SW. Bulgaria	Palamarev, 1970
	Pliocene	Ob R., Tomsk, W. Siberia, USSR	P. A. Nikitin, 1948
	Uncertain	W. Siberia, USSR	V. P. Nikitin, 1968
M. minor (Chandler) Eyde	Late Eocene	Barton Beds, England	Chandler, 1960
M. sibirica (P. A. Nikitin) Eyde	Oligocene	W. Siberia, USSR (6 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	W. Siberia, USSR	Dorofeev, 1963a
M. triangulata G. Bal., *nomen nudum*?	Unknown	W. Siberia, USSR	V. P. Nikitin, 1968
Mneme sp.	Miocene	W. Siberia, USSR	Dorofeev, 1963a
	Mid/Late Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969

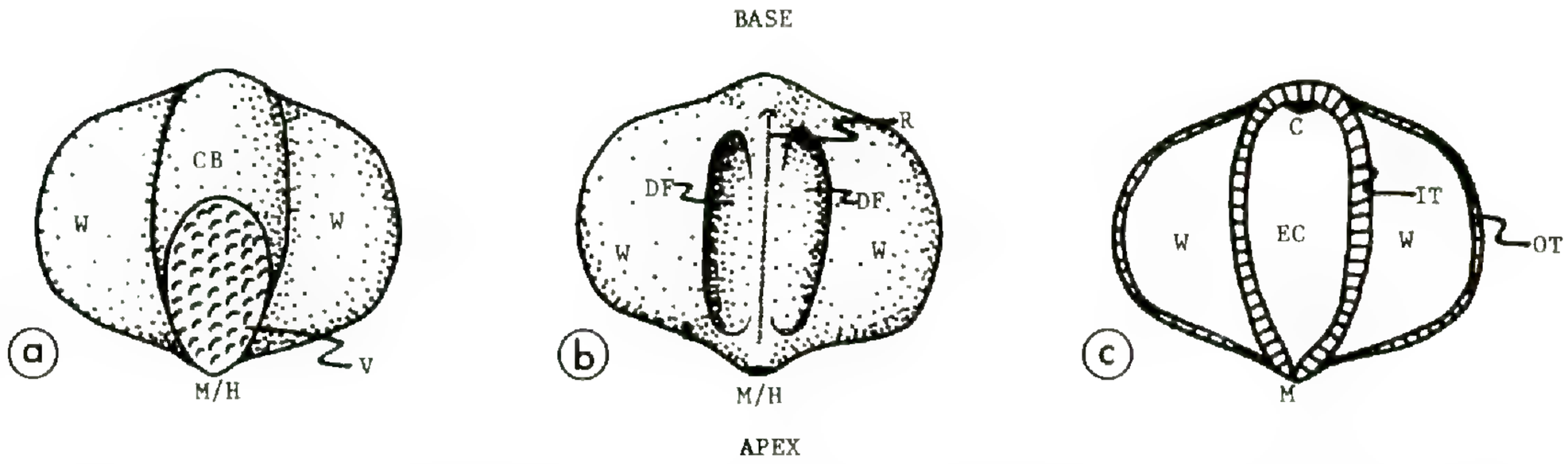

FIGURE 3. *Microdiptera parva:* a, ventral view; b, dorsal view. c, longitudinal section. CB = central body, W = wing, DF = dorsal furrow, other conventions as in FIGURE 1.

deep around the seed cavity. Near the germination valve it thickens and is formed of one to three layers of radially elongate sclereids, often with angular lumina indicating that crystals had once been present (PLATE III, H). Laterally, the outer integument is inflated by the intercalation of a zone of equiaxial spongy cells of 12–18 μm. diameter. This is bounded by a thin outer testa of one or two layers of weakly lignified small cells and the much thicker inner sclerotesta of the central body (FIGURES 3, c; 4, b). The inner integument is formed of elongate cells sheathing the inside of the embryo cavity. The foregoing description is based on published material and on the Brandon specimens.

There are six reported species of *Microdiptera*, although these can be reduced to two or perhaps even to one. The most common is *M. parva*, which is known from ten reports of Late Eocene to Middle Miocene age and, with the exception of the extension presented here, is restricted to western and central Europe. While *M. major* (Middle Eocene of southern England; one report) has distinctive mucrones on its apex and occasionally on its wing tips (e.g., Chandler, 1963b, *pl. 19, figs. 9–29*), similar features are sometimes seen in *M. parva* (Chandler, 1963a, *pl. 31, figs. 99–107*). Mai and Walther (1978) considered *M. major* to be a synonym of *M. parva*, noting that the two were separated by small characters that were seen to intergrade in large populations. *Microdiptera tavdensis* Dorofeev (Oligocene of the Urals; one report) is also quite similar to *M. parva*, and the present author concurs with Friis (1980) that the two likely represent a single species. *Microdiptera donata* (Holý) Tiffney (Miocene of Czechoslovakia; one report) was distinguished by Holý (1976) from specimens of *M. parva* that occurred in the same deposit. However, the morphology of *M. donata* overlaps with that of *M. parva* from Brandon, suggesting a degree of local variation in the latter species. Similarly, while *M. uralensis* (Miocene of the Urals; one report—a *nomen nudum*, see above) and *M. elongata* (Oligocene and Miocene of Siberia; three reports) are united by their narrow wings and elongate shape, both also overlap in morphology with the Brandon population of *M. parva*. An enumeration of the species in the literature is provided in TABLE 3, but it seems most likely that they may all be reduced to synonomy under *M. parva*, which may in turn ultimately be shown to be a species of *Mneme*.

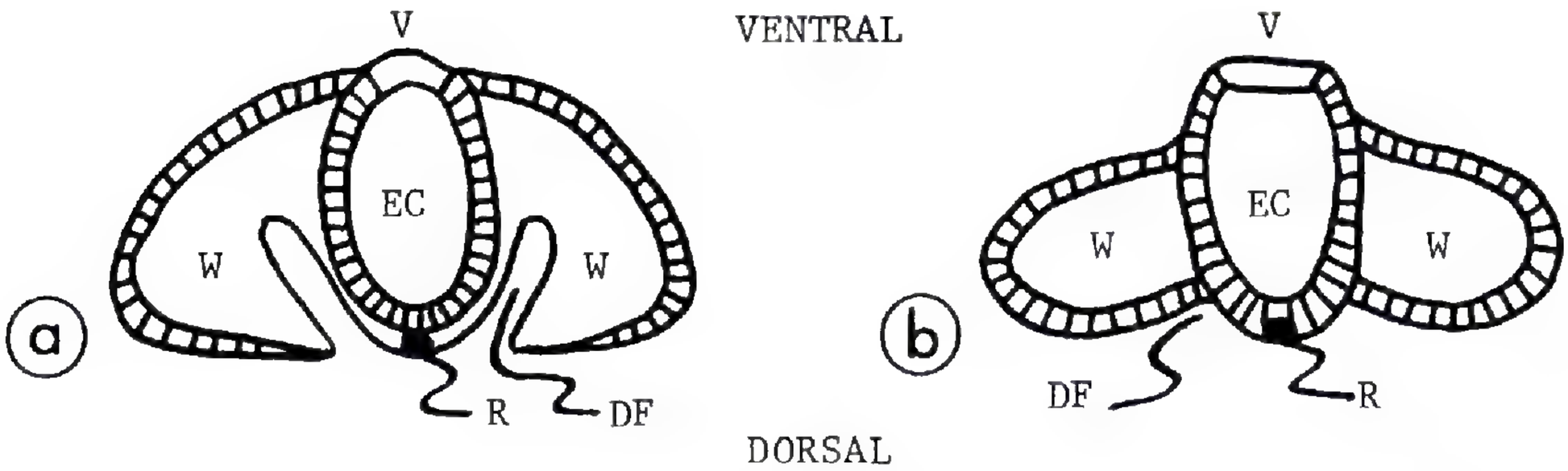

FIGURE 4. Cross sections (redrawn from Friis, 1980, with permission of author): a, *Mneme*; b, *Microdiptera*. Conventions as in Figures 1 and 3.

Alatospermum. The anatropous seeds of *Alatospermum* are similar to those of *Mneme* and *Microdiptera;* the fruit is not presently known. The seeds are dorsiventrally flattened and quite variable in shape, ranging from broadly triangular to nearly rectangular, often with a pointed apex and irregular lateral margins. The wings are completely lateral and are long, narrow, and thin; they are often missing or unequally developed on the two sides of the body. The seeds range from 0.75 to 1.55 mm. in length and from 0.85 to 1.8 mm. in width. The raphe runs from the apex to the basal chalaza along the dorsal sclerotesta of the central body; no flanking grooves are apparent. The elongate rectangular germination valve extends the full length of the seed and, depending on the degree of development of the wings, occupies one quarter to three quarters the width of the seed. Its surface is marked by six or seven longitudinal rows of pits about 50 μm. in diameter. At maturity the valve is reflexed, exposing the embryo cavity that extends the full length of the seed. The valve remains attached at its base to the seed. There is no obvious layer of epidermal tissue, and the structure of the inner and outer integuments has not been preserved. The genus is represented by *A. lakense* (one report) from the Lower Eocene of southern England (Chandler, 1962).

The foregoing summary of the seed characters of *Decodon, Mneme, Microdiptera,* and *Alatospermum* provides a basis for considering generic and specific delimitation. At the generic level, these distinctions can be tentatively summarized in a key, here adapted and modified from Chandler (1963b), Dorofeev (1968), and Mai and Walther (1978).

GENERIC KEY

A. Seeds lacking dorsal grooves, germination valve remaining attached to seed body at maturity.
  B. Seeds elongate, with lateral wings; germination valve extending full length of seed body. . . . . *Alatospermum.*
  B. Seeds rounded, lacking lateral wings; germination valve extending one half to two thirds length of seed body. . . . . *Decodon.*
A. Seeds with dorsal grooves, germination valve detaching completely from seed body at maturity.
  C. Lateral wings inflated, seed body buried in wings, dorsal grooves deep; ca. 20 rows of pits on germination valve. . . . . *Mneme.*

TABLE 3. **Reported species of Microdiptera.**

Species	Age	Locality	Citation
Microdiptera donata (Holý) Tiffney	Miocene	Zittau Basin, Czechoslovakia	Holý, 1976; present paper
M. elongata (Dorofeev) Dorofeev	Oligocene	Kompassky Bor, W. Siberia, USSR	Dorofeev, 1963a (see also Dorofeev, 1962, 1968)
	Miocene	W. Siberia, USSR (2 localities)	Dorofeev, 1963a (see also Dorofeev, 1962, 1968)
*M. major** Chandler	Mid Eocene	Bournemouth Freshwater Beds, England	Chandler, 1963b (but see Mai & Walther, 1978)
M. parva Chandler	Late Eocene	Highcliff Sands, Mudford, England	Chandler, 1963b
	Late Eocene	Lower Headon, Isle of Wight, England	Chandler, 1961b (see also Chandler, 1963b)
	Early Oligocene	Upper Headon, Isle of Wight, England	Chandler, 1963a
	Early/Mid Oligocene	Haselbach bei Dresden, E. Germany	Mai & Walther, 1978
	Mid Oligocene	Bovey Tracy, England	Chandler, 1957
	Miocene	Fasterholt, Denmark	Friis, 1980
	Miocene	Damgaard, Denmark	Friis, 1980
	Mid Miocene	W. Bulgaria	Palamarev, 1971
	Mid Miocene	Hrádek, Zittau Basin, Czechoslovakia	Bůžek *et al.*, 1964
	Mid Miocene	Hartau, E. Germany	Mai, 1964
M. tavdensis Dorofeev	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
M. uralensis (Dorofeev) Friis†	Early/Mid Miocene	Polevskoĭ, Ural Mts., USSR	Dorofeev, 1970 (see Friis, 1980)
Microdiptera sp.	Pliocene	Balkan Peninsula	Mai & Walther, 1978

*Placed in *M. parva* by Mai and Walther (1978).
†Provisional usage: *nomen nudum*.

C. Lateral wings flattened, seed body emergent from wings, dorsal grooves shallow; 5 to 10 (to 12) rows of pits on germination valve. . . . . *Microdiptera*.

It is clear that *Decodon* and *Alatospermum* can be separated from *Mneme* and *Microdiptera* on two good characters—ventral grooves and germination valve attachment. This negates Kirchheimer's (1935, 1957) supposition that reports of *Decodon globosus* from the Niederlausitz represented undeveloped or damaged seeds of *Mneme menzelii;* E. M. Reid (1927) clearly illustrated seeds from this locality with unattached germination valves. Further, the wings of *Alatospermum* indisputably separate it from *Decodon.*

It is far more difficult, however, to discern or defend the separation of *Microdiptera* and *Mneme.* Dorofeev (1963a) questioned the distinction between the two, and indicated in 1970 that the differences were insignificant, an opinion alluded to by Chandler (1963b). Mai and Walther (1978) unite the two genera, recognizing *Microdiptera* as a subgenus of *Mneme.* However, Friis (1980) rejects Mai and Walther's treatment and suggests that the two genera can be separated on three characters: number of pit rows on the germination valve (more than 20 in *Mneme,* 5 to 10 (to 12)) in *Microdiptera;* degree of submersion of the central body in the wing tissue (fully buried in *Mneme,* emergent in *Microdiptera*); and depth of the dorsal furrows (deep in *Mneme,* shallow in *Microdiptera*).

The stability of these characters is questionable. As noted above, some specimens identified as *Mneme menzelii* appear to have six to nine rows of pits on the germination valve. Either these are poorly illustrated or misidentified, or the character fails to hold. The degree of immersion of the central body in the wing tissue may be directly related to the degree of inflation of the wings; this seems particularly likely since many authors have mentioned that *Mneme* has thicker wings than *Microdiptera.* The variation in wing inflation and degree of emergence of the central body could be extremes of a developmental continuum. In addition, these features could be correlated with the depth of the dorsal furrows, reducing these three characters to one: the degree of development of the wings. In the present work, *Microdiptera* and *Mneme* are treated as separate genera, but only due to the absence of a first-hand, population-level investigation of the material involved. In all likelihood, Mai and Walther are correct in uniting these genera.

The preceding paragraphs involve morphological arguments for the recognition of a broad specific—and perhaps generic—concept in these genera. This conclusion is reinforced by features of the biogeography and ecology of modern-day aquatic and paludal plants. These plants commonly have very wide ranges, a fact first noted by Darwin (1859) and subsequently commented on by many authors (see Hutchinson, 1975). Indeed, Arber (1920) suggested that the range of the average aquatic plant species was greater than that of the average terrestrial species (e.g., *Potamogeton pusillus* L., *Phragmites communis* Trin.). A partial explanation for this pattern lies in the fact that bodies of fresh water are, with few exceptions, transitory in geologic time.

For this reason, successful aquatic plants must be fairly vagile, and thus capable of spreading to newly available habitats as they appear. This combination of vagility and discrete, isolated populations offers a unique situation for limited, but continuous, genetic exchange and local differentiation.

A body of fresh water offers an isolated, favorable environment to aquatic plants. A single disseminule or a small number of disseminules may become established in such a site and give rise to a large population by both sexual and asexual reproduction (Hutchinson, 1975). While the population is genetically linked to its parent source, the limited number of founding disseminules provides the opportunity for localized differentiation. Although this local differentiation may be balanced by a subsequent influx of disseminules or may be limited by the geologic duration of the water body, the entire system favors the appearance of spatially and temporally localized variants of an otherwise widespread species. In addition, while bodies of fresh water are unstable in a geologic sense, they are environmentally stable. As a result, they provide a buffered environment for growth when compared to terrestrial environments (Szafer, 1954; Hutchinson, 1975). This relative stability of environment suggests that the level of abiotic selective pressure is also relatively low. Further, this reduced level of selection pressure has probably not changed to any great degree in the last 50 million years. All of these factors argue for the stability of aquatic species over long periods of time.

It is suggested here that, in addition to a wider average range of distribution, aquatic vascular plants have a longer average species duration than terrestrial ones. This prediction can be tested in the fossil record (work in progress).

These considerations from extant aquatic plants argue for the use of a wide species concept in the identification of fossil remains of aquatics. Many of the distinctions between the various species of fossils of *Decodon*, *Microdiptera*, and (to a lesser degree) *Mneme* are not based on discrete characters, but on size and shape—characters that vary continuously. If one judges by the biological circumstances of modern aquatics, these characters cannot be seen as reliable, and it is not unreasonable to suggest that the number of species in these three genera could be reduced.

The foregoing discussion does not preface a formal revision of the three genera involved. Rather, it is intended to summarize the current state of affairs and to place the description of the Brandon material in perspective.

SYSTEMATICS

Lythraceae Jaume St.-Hil. Mém. Mus. Hist. Nat. Paris **3:** 377. 1815.

Microdiptera Chandler, Bull. Brit. Mus. (Nat. Hist.) Geol. **3:** 107. 1957.

Microdiptera donata (Holý) Tiffney, comb. nov.

Mneme donata Holý, Sborn. Nár. Mus. v Praze, Řada B, Přír. Vědy **32:** 1–13. 1976.

Holý (1976), while acknowledging the difficulty of distinguishing *Mneme* and *Microdiptera*, assigned these specimens to the former genus on the basis

of their "lack of perfect wings." The present author has no trouble in discerning narrow wings on the illustrated specimens (Holý, 1976, *pl. 1, figs. 17–22; pl. 2, figs. 1–9*) in light of the variation seen in the Brandon material. Further, the specimens display shallow dorsal grooves ("longitudinal lateral furrows on [the] margin occasionally"), and most importantly, the germination valve has eight rows of pits. If the generic distinction between *Microdiptera* and *Mneme* is to be recognized, then these specimens clearly show closer affinities with the former genus.

Microdiptera parva Chandler, Bull. Brit. Mus. (Nat. Hist.) Geol. **3:** 107. 1957. PLATES I, D–F; II, A–F; III, E–H.

Neither pollen (Traverse, 1955) nor wood (Spackman, 1949) of this family has previously been reported from the Brandon Lignite.

MATERIAL. Over 120 seeds have been collected from the silt facies of the Brandon Lignite; the seeds are common, and thousands more could be collected. The specimens are jointly assigned number 51391 of the Paleobotanical Collections of the Botanical Museum, Harvard University.

DESCRIPTION. No evidence of fruits was found. The seeds are bitegmic and anatropous. Their shape approximates that of a flattened and distorted hemisphere, the dorsal surface being flat and the ventral convex. In dorsal/ventral view the outline of the seeds varies greatly, depending upon the relative development of the wings. Elongate, angular, and smoothly rounded forms are all present (FIGURE 5). The seeds range from 0.85 to 1.3 mm. (mean, 1.02 mm.) in length and 0.6 to 1.3 mm. (mean, 0.95 mm.) in width. The raphe commences at the apex of the seed and passes along the dorsal face between the relatively deep furrows to the base, where it descends through the sclerotesta of the central body to the chalaza (PLATE II, F). The oblong, convex germination valve occupies one third to one half the

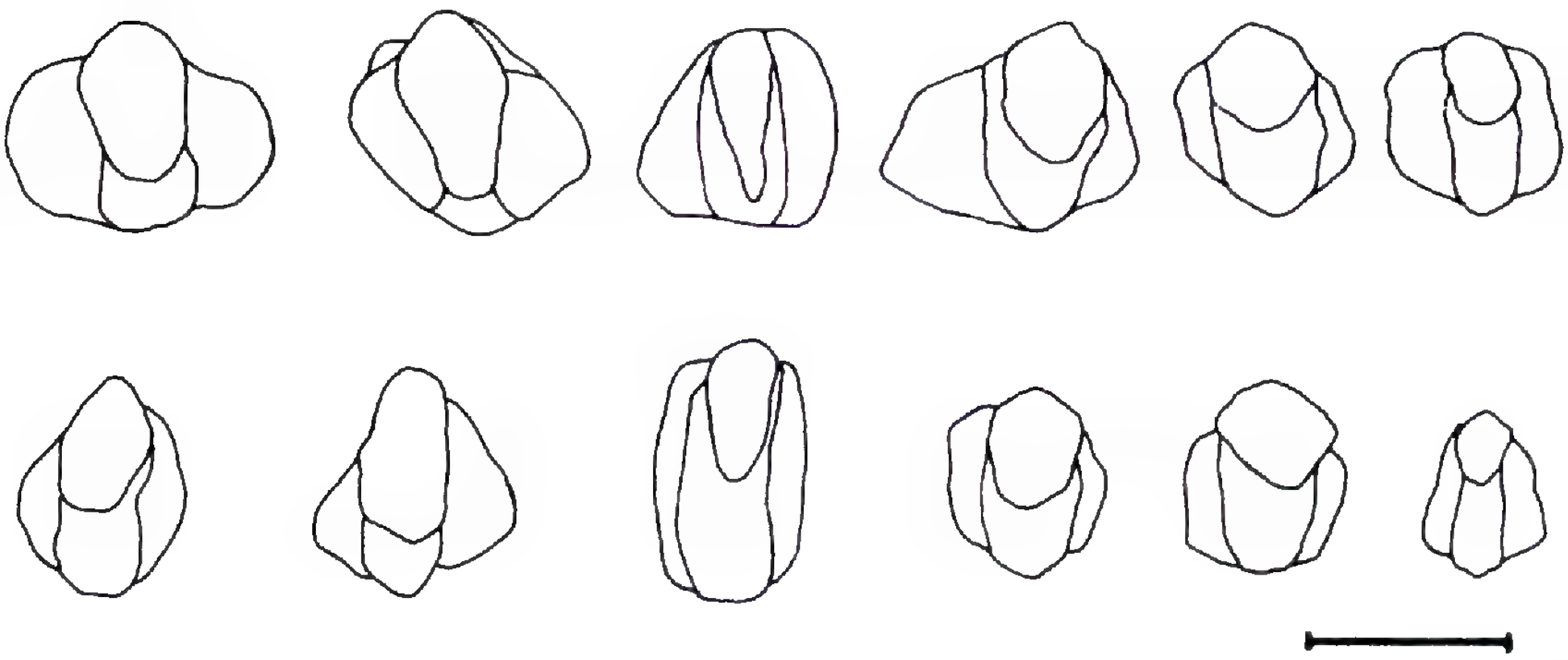

FIGURE 5. Outline drawings of *Microdiptera parva* from Brandon, demonstrating morphological variability. Ventral view, apex uppermost. Scale = 1 mm.

width of the ventral face, and one third to three quarters of its length (FIGURE 5). The surface of the valve is marked by seven to ten rows of equiaxial pits approximately 50 μm. in diameter. Upon dehiscence (PLATE II, A), the valve separates completely from the central body (PLATE II, C), splitting along a line of specialized sclereids around the margin of the valve (PLATE II, C, D). This exposes the ellipsoid embryo cavity, which extends the full length of the seed body. The epidermal tissue is not preserved. The outer integument is differentiated into two zones, one forming the central body (the inner sclerotesta), and the other a derived layer sheathing the wings (the outer sclerotesta) (PLATE III, E, F). The outer sclerotesta is frequently abraded off the surface of the wings (PLATE II, A, E) but is apparently formed of elongate sclereids. In the rare instances where this layer can be measured, it is 6–12 μm. thick and is composed of a single layer of cells. The 30–45 μm. thick inner sclerotesta sheathes the embryo cavity in one to three layers of cells that measure approximately 28 × 12–18 μm. In the vicinity of the germination valve, this layer thickens to 50–90 μm. and is formed of sclereids that commonly have angular lumina indicative of the presence of crystals (PLATE III, H). The spongy mesophyll between the inner and outer sclerotestae is restricted to the two wings and is composed of roughly isodiametric parenchyma cells 12–18 μm. in diameter (PLATES II, E; III, E, F). The inner integument is poorly preserved but consists of a single layer of narrow, elongate (3–5 × 40 μm.) cells (PLATE III, H).

AFFINITIES. The morphology of these seeds is in complete agreement with that of *Microdiptera* and falls within the range of *M. parva*. In light of the ecological/biogeographic observations on aquatics presented earlier, no reason is seen to erect a new species for this first North American report.

ECOLOGY. *Decodon, Microdiptera,* and *Mneme* tend to occur together at many European localities. P. A. Nikitin (1929) initially suggested that *Mneme* was usually found in the absence of *Decodon* in certain Siberian deposits, from which he concluded that the two genera were ecologically distinct. This appears to have been a function of the sample since a statistical examination of the 75 floras that bear *Mneme, Decodon,* and *Microdiptera* reveals that there is no significant negative correlation between any combination of the three genera. In general, all three are associated in the fossil record with communities and depositional environments derived from swamp or lakeside habitats, rather than from more mesic upland sites. An excellent example of this is found in Holý's study of the Miocene of Hrádek nad Nisou, Czechoslovakia (1975, 1976). The clear taxonomic and taphonomic association of the three genera suggests that extant *Decodon* may be taken as a common ecological model.

Decodon verticillatus is a deciduous perennial shrub of the margins of swamps, ponds, and streams from Nova Scotia, southwestern Quebec, and southern Ontario, south to Florida and eastern Texas (Correll & Correll, 1972; Graham, 1975). The seeds apparently germinate on banks; the branches of the resulting plant are weak and soon fall over (Sculthorpe, 1967; Hutchinson, 1975). If they fall into water, aerenchymatous tissue and roots are developed, leading to the formation of a mat. Leaf-bearing shoots arise from this mat,

ultimately to collapse and repeat the process. As a result, the plant achieves rapid vegetative spread, forming dense mats along waterways (Correll & Correll, 1972). The flowers are entomophilous (Hutchinson, 1975), although reduced flower size may presage a shift to self-pollination (Sculthorpe, 1967). The plant is higher in alkaloids than are most aquatics, perhaps as a result of its relative accessibility to herbivores (Hutchinson, 1975). *Decodon* is known to be transported both internally and externally by waterfowl (Ridley, 1930).

DISCUSSION

The discovery of *Microdiptera* at Brandon adds another genus to a growing list of taxa present in the Tertiary floras of both eastern North America and Europe, including *Magnolia* L. (Tiffney, 1977), an undescribed Brandon fruit similar to *Rehderodendron* Hu, and a recently discovered occurrence of *Wetherellia* Reid & Chandler and *Palaeowetherellia* Chandler from the Eocene of Virginia and Maryland (research in progress). This pattern is presumably a holdover from an early Tertiary floristic exchange across the North Atlantic (Tiffney, 1980b). *Decodon* provides a modern counterpoint to this pattern, having been widely distributed in the European Tertiary but presently persisting only in eastern North America. Presumably *Decodon* and *Microdiptera* coexisted in the North American Tertiary, but only *Decodon* survived the Quaternary.

A concluding speculative remark on phylogeny: the earliest of the four related genera is *Alatospermum,* which has the characters of both *Decodon* and *Microdiptera/Mneme. Alatospermum* could thus be considered as ancestral to the other three genera, giving rise to the *Decodon* morphology in the Late Eocene through supression of the wing tissue, and to *Microdiptera* in the Late Eocene through complete detachment of the germination valve. *Mneme* could have been derived from *Microdiptera* in the Oligocene by very **minor deve**lopmental changes.

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EXPLANATION OF PLATES

PLATE I

FIGURES A–C. Seeds of *Decodon verticillatus*, covered by cuticle. A, dorsal view, apex down (*Rehder 1297*). B, apical/dorsal view: hilum a clear circular hole; micropyle ventral to it, less well defined. C, ventral view, apex up: separation between weakly developed lateral wings and central body can be seen; germination valve in upper half of central body.

FIGURES D–F. Seeds of *Microdiptera parva* from Brandon. D, seed of average shape, ventral view, apex down. E, semi-elongate seed, ventral view, apex to left: cellular depressions on germination valve distinct. F, seed with unequally developed wings, central body displaced to one side, ventral view, apex down. Scales = 100 μm.

PLATE II

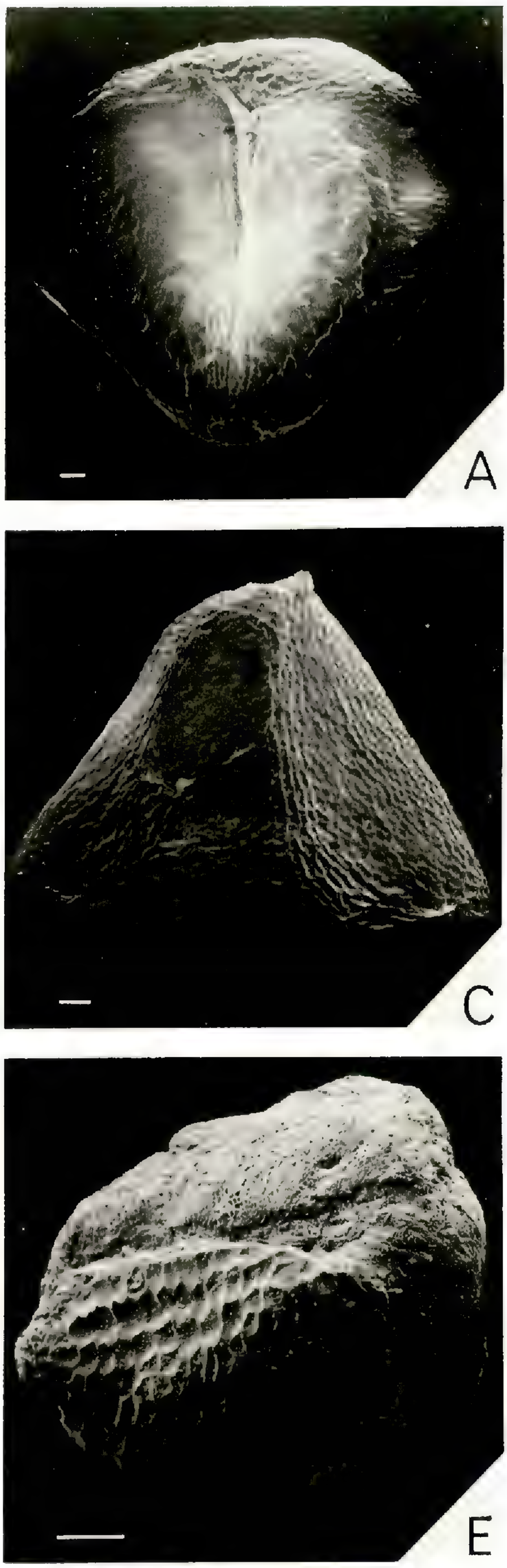
FIGURES A–F. Seeds of *Microdiptera parva* from Brandon. A, lateral view, apex to right: germination valve starting to dehisce (note striations on outer surface of central body and their absence due to abrasion on near wing, exposing underlying spongy cells). B, ventral germination valve, apex to right. C, apical/ventral view: germination valve lost, exposing embryo cavity (ringed by cells of marginal zone of dehiscence). D, detail of dehiscence zone, apical view: embryo cavity to right, exterior to left. E, detail of outer ventral surface, apex to left: elongate elements of outer sclerotesta clear on central body and in some places on wing; cells of spongy mesophyll (exposed by abrasion) to lower right. F, dorsal view, apex to left: two dorsal furrows flanking path of raphe, which runs from apical hilum to small, subbasal depression leading to chalaza. Scales = 100 μm. in A–C, E, F; 10 μm. in D.

PLATE III

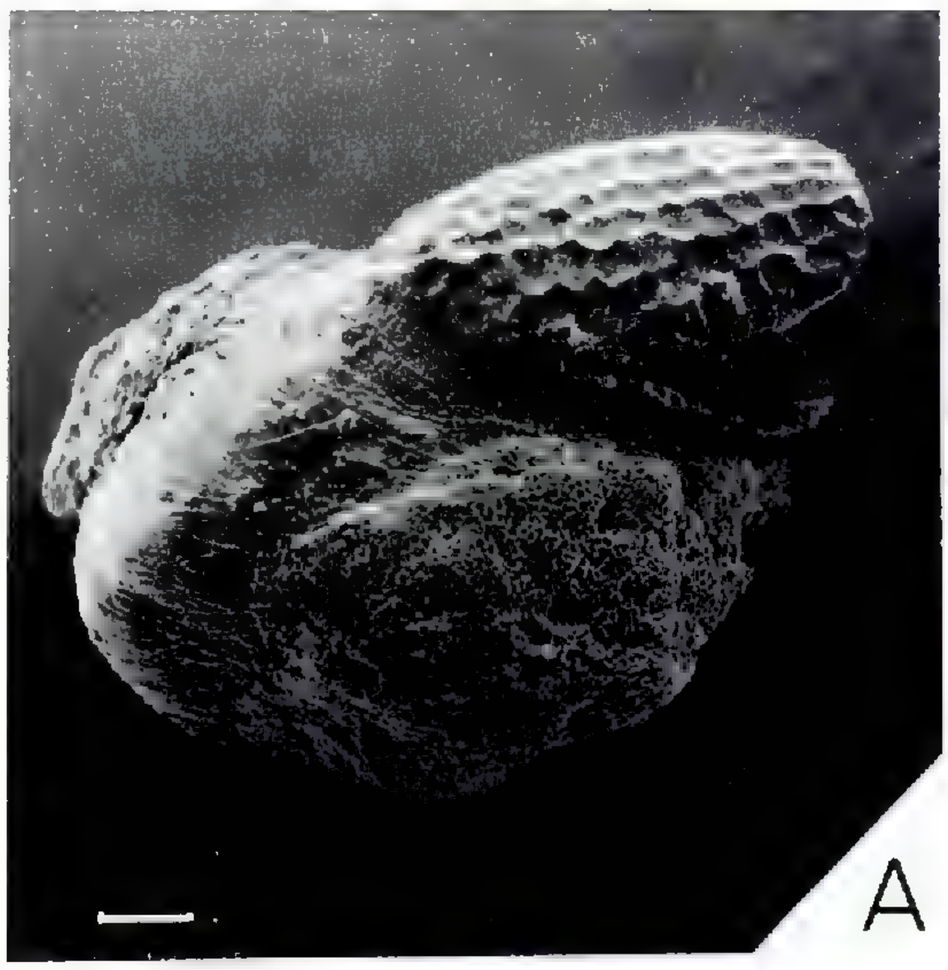
FIGURES A–C. *Mneme menzelii* from Frecheu, Germany (Miocene): A, ventral view, × 1.7, apex down; B, dorsal view, × 1.7, apex down, showing two dorsal furrows; C, cross section, × 542, embryo cavity to left (note thick inner sclerotesta and thin outer).

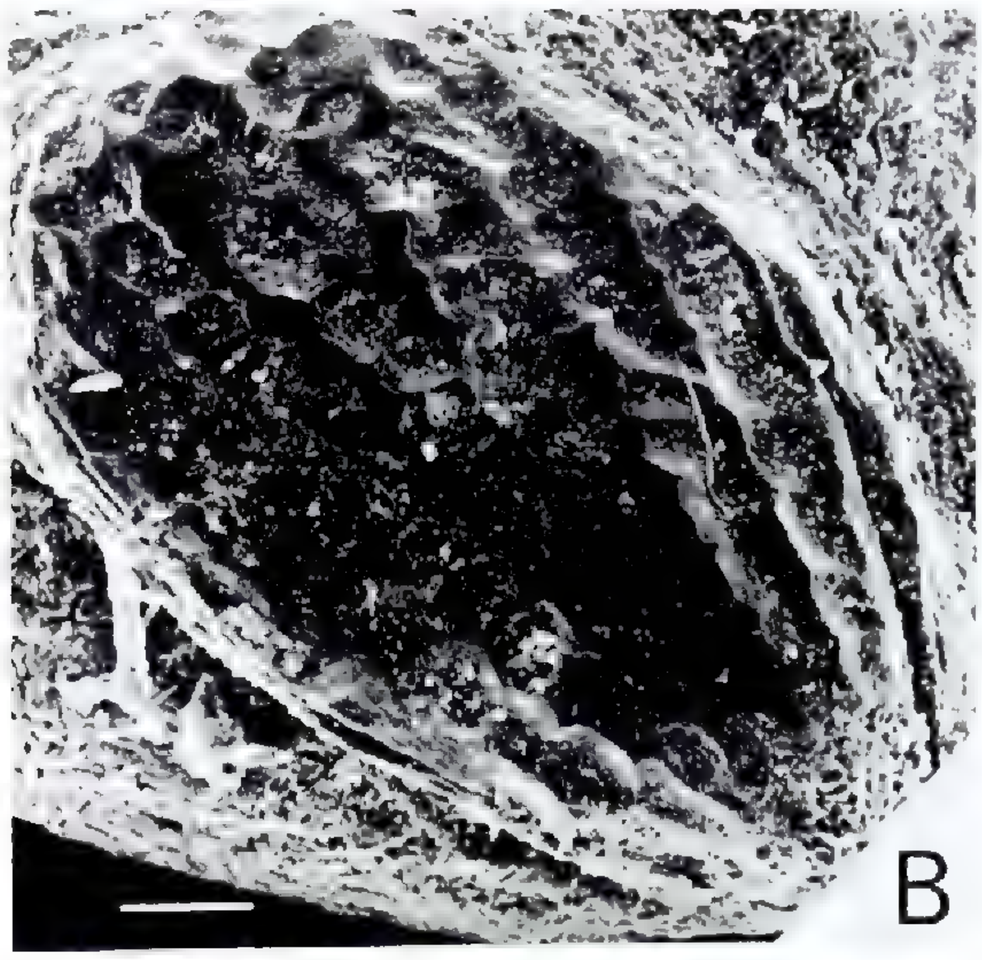
FIGURE D. *Decodon verticillatus* (*Rehder 1297*), cross section, × 37, ventral side up (note thin external sclerotesta and thick inner).

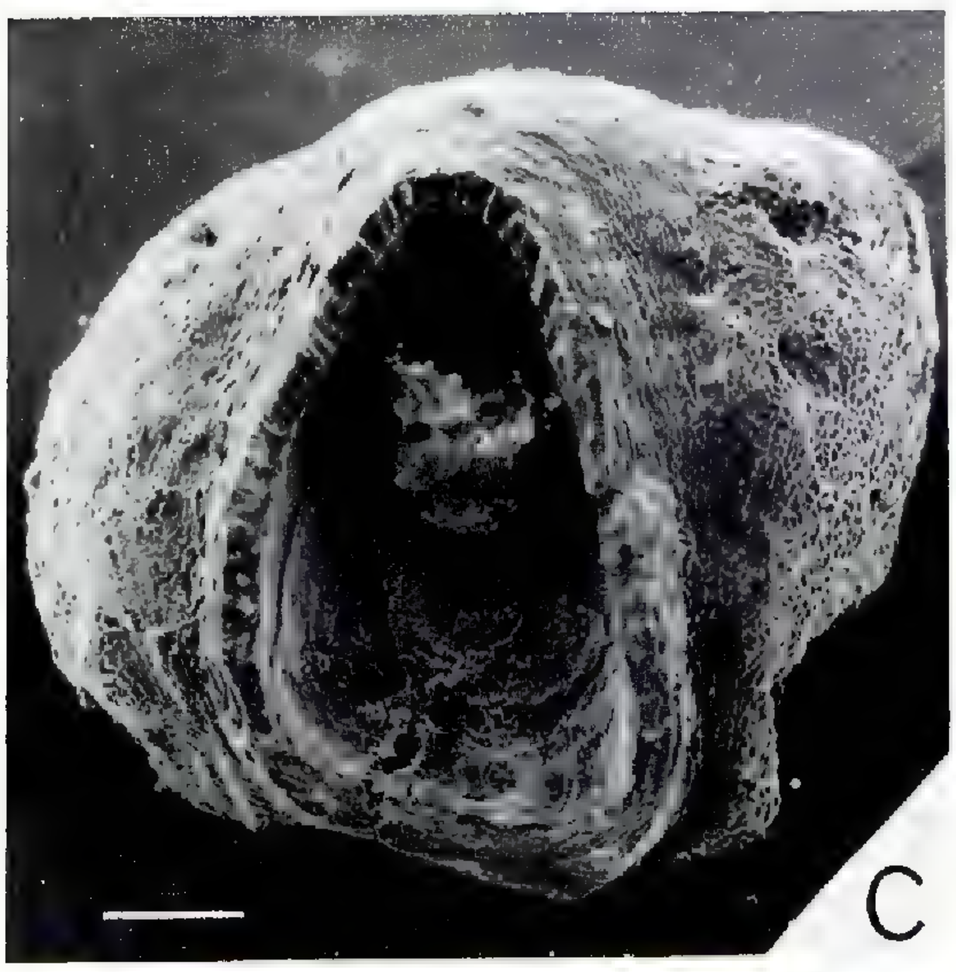
FIGURES E–H. *Microdiptera parva* from Brandon: E, cross section, × 66, ventral side up (note thin outer sclerotesta, thick inner sclerotesta, and spongy tissue of wings); F, longitudinal section, × 66, apex up, well-developed wings clearly evident; G, inner integument cells, × 490; H, detail of inner sclerotesta beneath germination valve, × 490, showing angular sclereid lumina indicative of crystal inclusions.

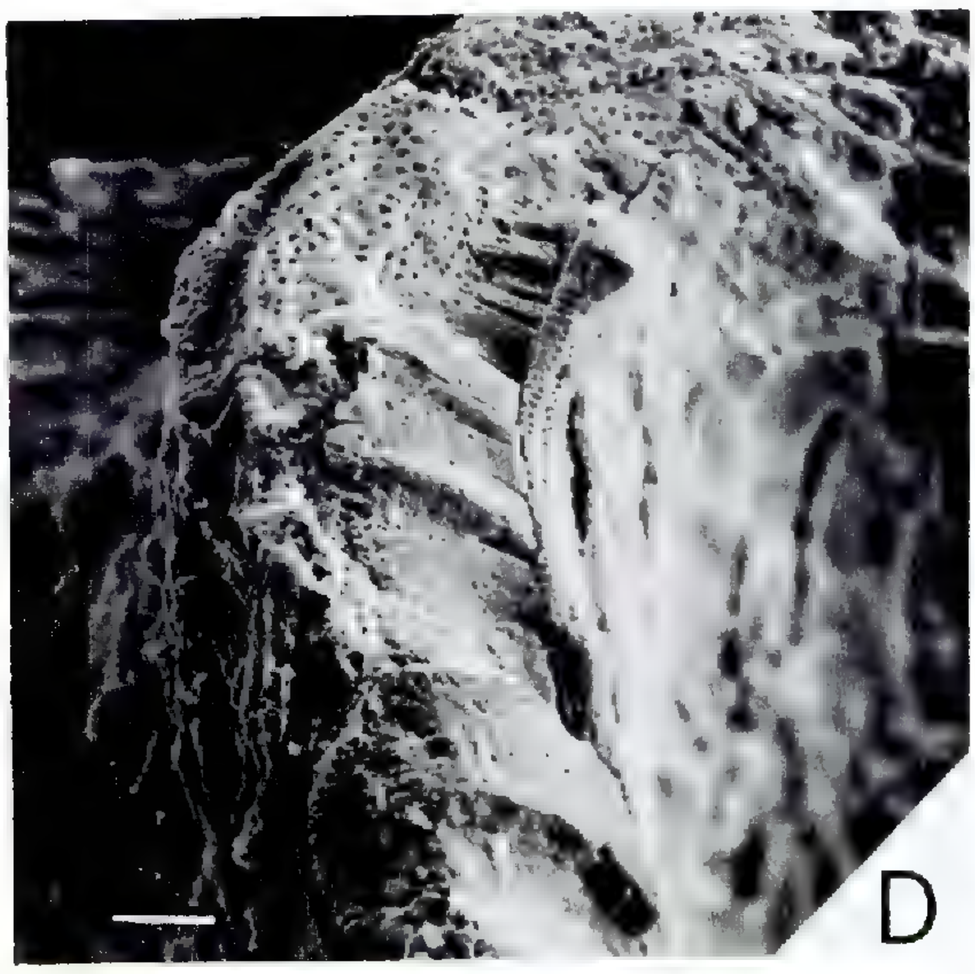


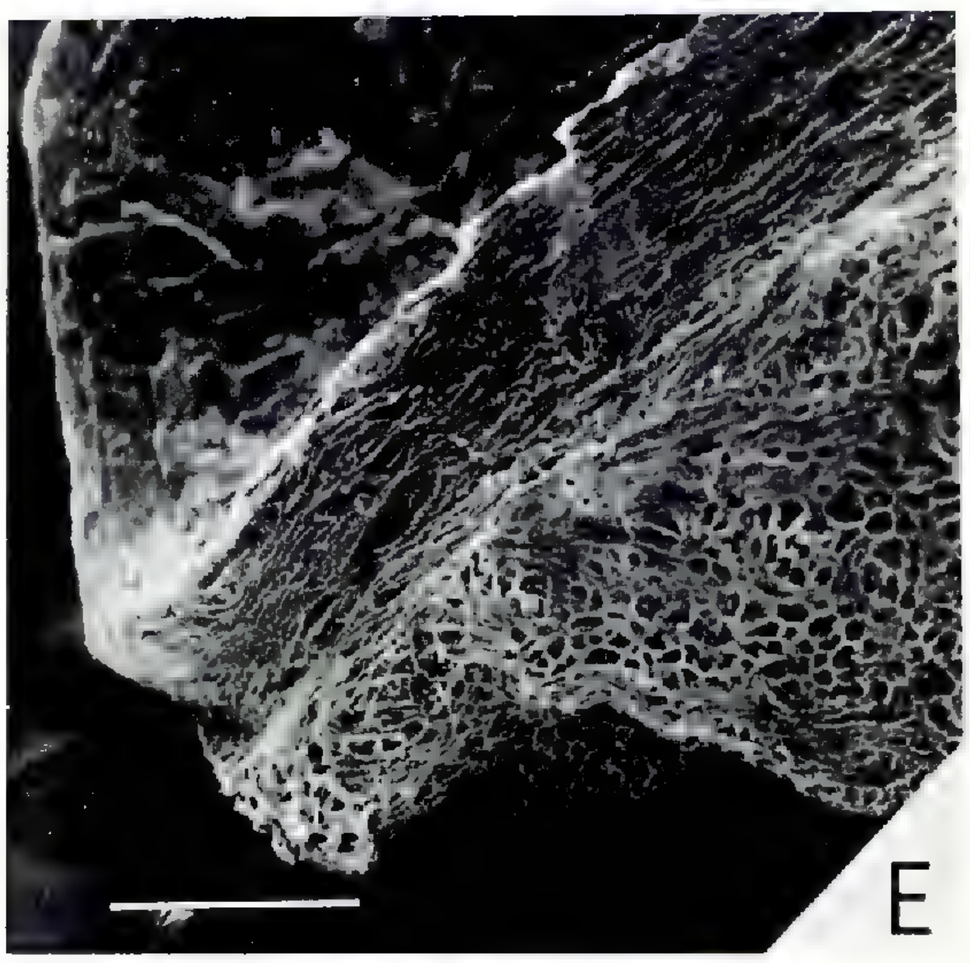
TIFFNEY, BRANDON LIGNITE, VI



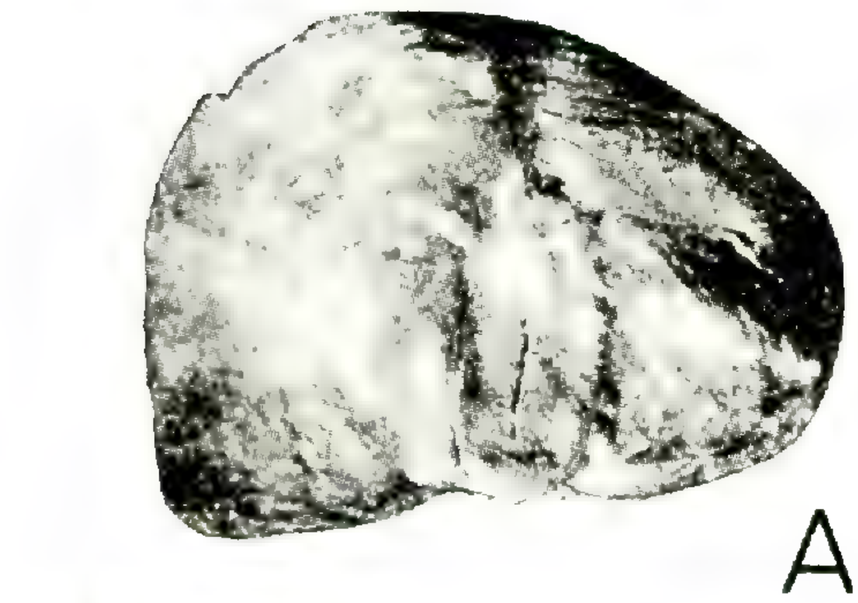








TIFFNEY, BRANDON LIGNITE, VI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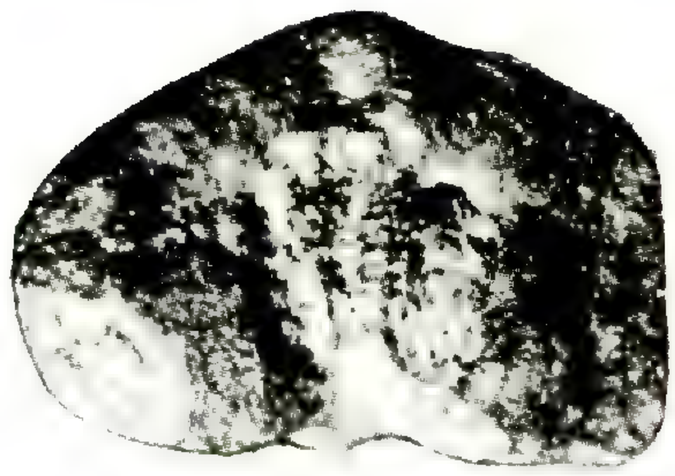
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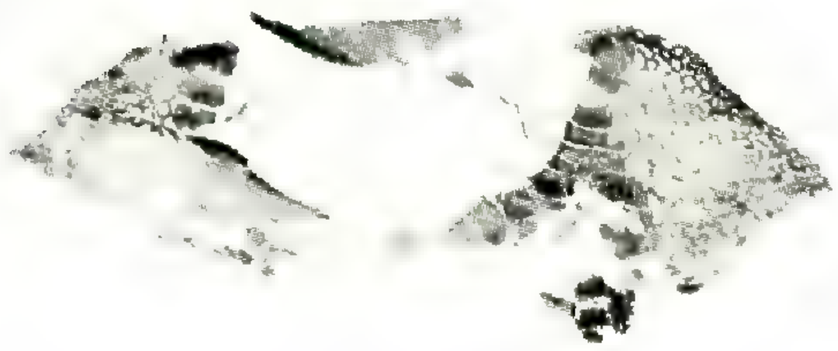
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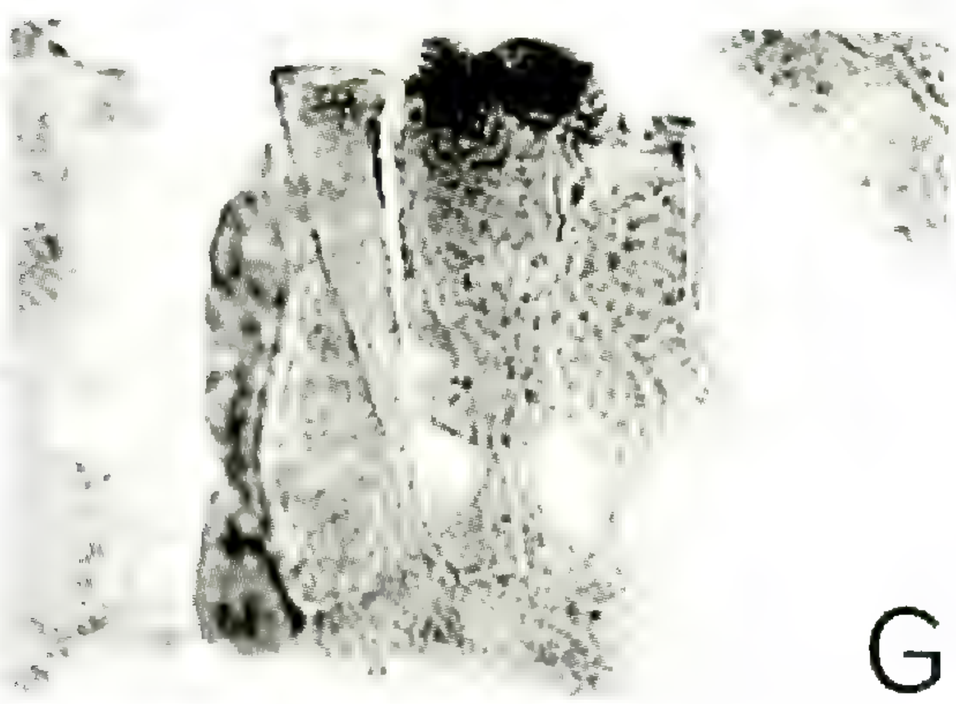
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TIFFNEY, BRANDON LIGNITE, VI

WEEDS OF THE CRUCIFERAE (BRASSICACEAE) IN NORTH AMERICA[1]

REED C. ROLLINS

THERE ARE NUMEROUS definitions of weeds (see Harlan & deWet, 1965; King, 1966), and the number of taxa included below could be greatly altered depending on one's concept of a weed. It is not my intention to become embroiled with the different interpretations of weeds. Rather, my primary purpose is to delineate the alien members of the Cruciferae that have become weedy in North America and to give their accepted botanical names. Sometimes these weeds are pestiferous as far as man is concerned, sometimes not. Their importance is often associated with the effect they have in displacing native species in habitats where alien and native species are in competition. Secondarily, I have listed native species that have become weedy. Few, if any, of these have become pestiferous.

A complete, up-to-date listing of weed species of the Cruciferae is not available in one place, although if one had prior knowledge of those that are alien or weedy such a list could be extracted from Kartez and Kartez (1980). Weed names determined by a subcommittee on standardization of common and botanical names (Anonymous, 1966) include many entries from the Cruciferae, but the list is incomplete and the most acceptable nomenclature is not always followed. My objectives have been to provide a listing of the taxa by their authentic botanical names, to give synonymy where required for clarification of the accepted name, to provide notes on distribution and abundance, and to present miscellaneous notes that are deemed to be of interest. The genera are listed alphabetically, as are the infrageneric taxa under each genus. The chromosome number, when known, is given for each taxon, and the leading synonym, if there is one, is given in parentheses after the accepted name. Species considered to be noxious are marked with an asterisk.

Those native species of the Cruciferae that have weedy tendencies and by many criteria might be classed as weeds are given in the second part of the paper. Because of my special knowledge of the family as it occurs in North America, I have presented information in that section that is not available in the literature. None of the native species is in the category usually described as noxious. A few species approach this rating but fall short because they do not seriously interfere with farming or other plant cultural practices. In time, as happened in a much earlier period in the Old

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World, these native species may adapt better to the more open habitats provided by deforested and disturbed lands and may become weeds in the fullest sense of the word.

ALIEN WEEDS OF THE CRUCIFERAE

Alliaria petiolata (Bieb.) Cavara & Grande (*A. officinalis* Andrz.)—GARLIC MUSTARD. Annual or biennial. Near habitation, roadsides, waste places, alluvial woods, and fields; usually in shade or moist habitats. Quebec to British Columbia and Oregon; Kansas to North Carolina and northward. Native of Europe and Asia; old English garden plant. $n = 21$ (Easterly, 1963); $2n = 36$ (Mayor, 1934); $2n = 42$ (Jaretsky, 1932).

***Alyssum alyssoides** (L.) L.—PALE ALYSSUM. Annual or biennial. Roadsides, disturbed sandy or gravelly banks, waste places, overgrazed mountain meadows, and dry hillsides. Widely dispersed in North America, Newfoundland to Alaska, California to Virginia. Native of Europe and Asia. $n = 16$ (Mulligan, 1964); $2n = 32$ (Manton, 1932).

***Alyssum desertorum** Stapf. Annual. Open desert or semidesert and disturbed grassland, roadsides, and waste places. Southern Manitoba to Alberta; Washington to Nebraska. It has become abundant on sheep rangelands in the Rocky Mountain and Great Basin region. Native of eastern Europe and western Asia. $n = 16$ (Mulligan, 1964); $2n = 32$ (Ančev, 1975).

Alyssum minus (L.) Rothm. var. **micranthum** (Meyer) Dudley. Annual. Roadsides, waste places, foothills, and open rangeland. Western United States in limited areas, particularly in the Rocky Mountain and Great Basin region. Native of Eurasia.

Alyssum strigosum Banks & Solander. Annual. Disturbed areas. Sporadic in western Nevada and west-central California. Native of Eurasia.

Alyssum szowitsianum Fischer & Meyer. Annual. Disturbed areas in the foothills and canyons of the Wasatch Range, northern Utah. Native of Eurasia.

Arabidopsis thaliana (L.) Heynh.—THALE CRESS, MOUSE-EAR CRESS. Annual. Gardens, old fields, river bottoms, roadsides, and waste places. Abundant and widespread nearly throughout North America. Used in experimental physiology, biochemistry, and genetics. Native of Europe and Asia. $2n = 10$ (Mulligan, 1964).

***Armoracia rusticana** Gaertner, Meyer, & Scherb. (*A. lapathifolia* Gilib.)—HORSERADISH. Perennial. Escaped from cultivation; usually in moist habitats, roadsides, ditches, waste places, and persisting in old gardens; difficult to eradicate. Throughout temperate and northern North America. Native of Europe and Asia. $n = 14, 16$ (Easterly, 1963); $2n = 32$ (Manton, 1932).

Aubrietia deltoidea (L.) DC. Perennial. Escaped from cultivation. Known from only a few localities in the United States. One station, at the top of

Hull Mountain in the Mendocino National Forest of California, is remote from gardens and cultivated areas. Native of Europe.

Aurinia petraea (P. Ard.) Shur (*Alyssum petraeum* P. Ard.). Perennial. Escaped from cultivation; shade of cliffs, Oneida County, New York. Native of Europe.

Barbarea verna (Miller) Ascherson—EARLY WINTER CRESS, SCURVY GRASS. Biennial or perennial. Sometimes grown as a salad plant; escaped from cultivation and naturalized. Connecticut to British Columbia, California to Florida. Native of Eurasia. $2n = 16$ (Manton, 1932).

***Barbarea vulgaris** R. Br.—COMMON WINTER CRESS, YELLOW ROCKET. Biennial or perennial. Roadsides, pastures, fallow and cultivated fields, open woods, and waste places. Difficult to eradicate in some habitats. Reproduced both by seeds and cauline rosettes. Several varieties. Common throughout temperate North America. Native of Europe and Asia. $n = 8$ (Easterly, 1963); $2n = 16$ (Manton, 1932; Mulligan, 1959).

***Berteroa incana** (L.) DC.—HOARY ALYSSUM. Annual or biennial. Dry waste places, fields, meadows, roadsides, and dry stream bottoms. General but sporadic in temperate northern North America. Very abundant in some localities. Native of Europe. $n = 8$ (Jaretsky, 1928); $2n = 16$ (Manton, 1932; Mulligan, 1957).

Berteroa mutabilis (Vent.) DC.—HOARY ALYSSUM. Annual or biennial. Roadsides, fields, and waste places. Uncommon and local. Widely separated places in the United States. Native of Europe.

***Brassica campestris** L.—FIELD MUSTARD, BIRD'S RAPE. Annual or winter annual. Sometimes (particularly in an earlier period) grown as a salad plant; escaped from cultivation or introduced as a seed contaminant. Especially common in grain fields in certain areas, it occurs in other cultivated or fallow fields, orchards, gardens, roadsides, waste places, and disturbed areas. Common and widespread throughout temperate North America including the highland areas of Mexico and Central America. Native of Eurasia. $n = 10$ (Harberd, 1972); $2n = 20$ (Mulligan, 1959).

***Brassica elongata** Ehrh. Perennial. Recently found as a roadside weed in eastern Nevada. It has begun to penetrate the open desert from disturbed roadside sites. The Nevada plants belong to subsp. *integrifolia* (Boiss.) Breistr. Native of western Asia and eastern Europe. $n = 11$ (Harberd, 1972); $2n = 22$ (Manton, 1932).

***Brassica juncea** (L.) Czern.—CHINESE MUSTARD, INDIAN MUSTARD. Annual. Escaped from cultivation or introduced as a seed contaminant. Common in grain fields and other fallow or cultivated fields; roadsides and waste places. Widespread in temperate North America including the highlands of Mexico and Central America. Native of Asia. $n = 18$ (Harberd, 1972); $2n = 36$ (Mulligan, 1959).

Brassica napus L.—RAPE. Annual. Escaped from cultivation. Waste places.

Sporadic in temperate North America. Native of Eurasia. $n = 19$ (Harberd, 1972); $2n = 38$ (Howard, 1938).

***Brassica nigra** (L.) W. D. Koch—BLACK MUSTARD. Annual. Escaped from cultivation or introduced in fields as a seed contaminant. Common in fields, orchards, and gardens; roadsides and waste places. Especially common in the Central Valley of California, where it was apparently introduced by the early missionaries. Widespread in temperate North America including cultivated areas of Mexico and Central America; somewhat more sporadic in the more northerly areas of the continent. Native of Eurasia. $n = 8$ (Harberd, 1972); $2n = 16$ (Manton, 1932).

***Brassica rapa** L.—BIRD'S RAPE. Annual. Escaped from cultivation or introduced in fields as a seed contaminant. Cultivated fields and waste places. Temperate North America including the highland areas of Mexico and Central America. Native of Europe. $n = 10$ (Aryavand, 1977); $2n = 20$ (Mitsukuri, 1957).

***Brassica tournefortii** Gouan. Annual. Roadsides, waste places, old fields, and open desert. Locally abundant in the desert counties of southern California and southern Nevada, spreading eastward in Arizona and southward in Baja California. Native of the Mediterranean region. $n = 10$ (Sikka, 1940).

Bunias orientalis L. Biennial or perennial. Meadows and waste places; sporadic in widely separated areas. Temperate northern North America, Nova Scotia to British Columbia, northern United States. Native of Eurasia. $n = 7$ (Laane, 1971); $2n = 14$ (Hindakova & Cincura, 1967).

Bunias erucago L. Annual or biennial. Waste ground and old fields. Local in Pennsylvania and Virginia. Native of Europe.

Cakile maritima Scop.—SEA ROCKET. Annual. Dunes and strand. Naturalized along the west coast of North America from British Columbia to Baja California, sporadic along the east and gulf coasts. Native of Europe. $n = 9$ (Shive, 1969).

Calepina irregularis (Asso) Thell. Annual or biennial. Cultivated and fallow fields. Infrequent. Virginia and North Carolina. Native of Eurasia. $2n = 28$ (Larsen & Lagaard, 1971).

Camelina alyssum (Miller) Thell. (*C. dentata* (Willd.) Pers.)—FLAT-SEEDED FALSE FLAX. Annual. Fields and waste places. Infrequent in southern Canada. Native of Europe. $2n = 40$ (Manton, 1932).

***Camelina microcarpa** Andrz.—LITTLEPOD FALSE FLAX. Annual. Seed contaminant of flax and grain. Roadsides, cultivated fields (particularly grain and flax fields), meadows, open prairie, waste places. General in North America but most common in western Canada and northwestern United States. Native of Asia. $n = 8$ (Easterly, 1963); $2n = 40$ (Mulligan, 1957; Manton, 1932).

***Camelina sativa** (L.) Crantz—FALSE FLAX. Annual. Seed contaminant of flax and grain. Grain and flax fields, roadsides, meadows, waste places. General

in temperate northern North America but less common than *C. microcarpa*. Native of Eurasia. $2n = 28$ (Mayor, 1934); $2n = 40$ (Manton, 1932).

***Capsella bursa-pastoris** (L.) Medicus—SHEPHERD'S PURSE. Annual. Cultivated and waste areas, street and road margins, gardens and lawns, orchards and vineyards, coffee plantations, and pastures. Cosmopolitan in temperate North America including most populated areas of Mexico and Central America. One of the commonest, nearly worldwide weeds. Native of Europe. $n = 8, 16$ (Easterly, 1963); $n = 16$ (Aryavand, 1977); $2n = 32$ (Mulligan, 1957).

Capsella gracilis Gren. Annual. Cultivated or disturbed areas. Known at present only from Virginia. Native of Europe. There is a question as to whether this is a species or a hybrid involving *C. bursa-pastoris* and *C. rubella*.

Capsella rubella Reuter. Annual. Waste places. Infrequent in widely separated places. Labrador to Alaska, southeastern United States including Florida. Native of Eurasia. $2n = 16$ (Hill, 1927; Queiros, 1973).

Cardamine hirsuta L.—HOARY BITTER CRESS. Annual. Gardens, lawns, fields, waste places; usually in damp or wet soil. Sporadic in much of temperate North America but common and abundant in southern and southeastern United States, where it is a winter annual and invades untilled fields. Present but uncommon in Mexico. Native of Eurasia. $n = 8$ (Bell, 1965); $2n = 16$ (Rollins & Rüdenberg, 1977; Mulligan, 1965).

Cardamine impatiens L. Annual or biennial. Shady grasslands and disturbed moist sites. Sporadic and uncommon. New Hampshire to Michigan and West Virginia. Native of Europe. $2n = 16$ (Manton, 1932; Lövqvist, 1957).

Cardamine pratensis L.—CUCKOO FLOWER. Perennial. Escaped from cultivation, in wet meadows. The typical form that has given rise to the cultivated one, which is also weedy, is native to Europe and Asia. Native infraspecific taxa occur in northern United States south to Virginia and from Labrador across Canada to Alaska. $n = 15, 28$ (Hussein, 1955); $2n = 16, 30, 44, 56, 64, 72, 76, 80$, ca. 96 (Lövqvist, 1956).

***Cardaria chalepensis** (L.) Hand.-Mazz. (*C. draba* (L.) Desv. var. *repens* (Shrenk) Rollins)—LENS-PODDED HOARY CRESS, WHITE TOP. Perennial. Fields, ditches, roadsides, and pastures; favors saline soils, particularly in irrigated farmlands. Abundant in the irrigated districts of western Canada and western United States; less common and more sporadic elsewhere. Very difficult to eradicate and considered to be noxious by all standards. Native to western Asia and probably the Middle East. $2n = 80$ (Mulligan & Frankton, 1962).

***Cardaria draba** (L.) Desv.—HEART-PODDED HOARY CRESS, WHITE TOP. Perennial. Fields, ditches, pastures, roadsides, and waste places. Most abundant in irrigated areas where saline soils are prevalent. Common in western Canada and western United States; less common but sporadically present in most parts of temperate Canada, United States, and Mexico. Very difficult to eradicate, noxious. Hybridizes with *C. chalepensis*. Native of Eurasia. $2n = 64$ (Manton, 1932; Mulligan & Frankton, 1962).

Cardaria pubescens (C. A. Meyer) Jarmolenko (*Hymenophysa pubescens* C. A. Meyer)—GLOBE-PODDED HOARY CRESS, WHITE TOP. Perennial. Fields, ditches, pastures, roadsides, and waste places. Most abundant in irrigated areas where saline soils are prevalent; common but less abundant than the other species of *Cardaria* listed above. Western Canada and western United States. Sporadic elsewhere in North America. An aggressive, noxious weed that is difficult to eradicate. Native of central and western Asia. $n = 18$ (Hanelet, 1973); $2n = 16$ (Mulligan & Frankton, 1962).

Chorispora tenella (Pallas) DC.—BLUE MUSTARD. Annual or winter annual. Roadsides, fields, waste places, and open rangelands. Very abundant in the western plains states and the intermountain area of western United States to southern Canada. Sporadic elsewhere in temperate North America. Native of southwestern Asia and the Middle East. $n = 7$ (Rodman & Bhargava, 1976); $2n = 14$ (Jaretsky, 1929; Manton, 1932).

Conringia orientalis (L.) Dumort.—HARE'S-EAR MUSTARD. Annual or winter annual. Grain fields, cultivated lands, roadsides, waste places, and open, disturbed places. Most common in the plains and prairie provinces of Canada and the plains states of the United States but frequently found in or near cultivated land elsewhere in North America. It is sometimes found in remote places in the mountains where mining ghost towns or other disturbances provide suitable habitats. Native of Eurasia. $n = 7$ (Aryavand, 1977); $2n = 14$ (Jaretsky, 1928; Löve & Löve, 1956).

Coronopus didymus (L.) J. E. Sm.—SWINE CRESS, WART CRESS. Annual or winter annual. Gardens, old fields, roadsides, street margins, and other disturbed sites in cities and towns. Troublesome in gardens and nurseries. Widespread and locally abundant in much of the inhabited parts of North America, especially in the central, eastern, and extreme western parts of the continent; less common but present in Mexico and Central America. Native of Eurasia. Sometimes stated or inferred (Smith, 1952; Ball, 1964) to be a native of South America; this seems unlikely. $n = 16$ (Rollins & Rüdenberg, 1977); $2n = 32$ (Jaretsky, 1932; Manton, 1932; Heiser & Whitaker, 1948).

Coronopus squamatus (Forskål) Ascherson (*C. procumbens* Gilib.)—CREEPING WART CRESS. Biennial or perennial. Ballast and waste places. Local at San Francisco and Portland on the west coast and on port ballast at several locations in eastern North America. Recent collections infrequent. Native of Europe. $2n = 32$ (Jaretsky, 1932; Manton, 1932).

Crambe maritima L.—SEA KALE. Biennial or perennial. Nursery areas and cliffs at only a few locations on the west coast of North America. Recent collections not seen. $n = 30$ (Jaretsky, 1932); $2n = 60$ (Manton, 1932).

***Descurainia sophia** (L.) Webb—TANSY MUSTARD, FLIXWEED. Annual or winter annual. Abundant in disturbed waste places, cultivated fields, roadsides, canyon bottoms, and open, dry, heavily grazed rangelands. Throughout temperate North America. Native of Eurasia. $n = 14$ (Rodman, 1978); $2n = 20$ (Mayor, 1934); $2n = 28$ (Manton, 1932; Mulligan, 1961b).

Diplotaxis erucoides (L.) DC. Annual or biennial. Ballast and waste places near ports. Local at a few places on the east coast of North America. Native of Europe. $n = 7$ (Jaretsky, 1932).

***Diplotaxis muralis** (L.) DC.—SAND ROCKET, STINKING WALL ROCKET. Annual or biennial. Waste places, roadsides, abandoned land, heavily grazed grassland, beaches, and around buildings; locally abundant especially in irrigated areas. Widely scattered in Canada, the United States, and Mexico. Native of Europe. $n = 21$ (Harberd, 1972); $2n = 22$ (Jaretsky, 1932); $2n = 42$ (Löve & Löve, 1944; Ibarra & La Porte, 1947; Harberd & McArthur, 1972).

Diplotaxis tenuifolia (L.) DC.—SLIM-LEAF WALL ROCKET. Perennial. Wasteland near seaports, coastal areas, roadsides, and waste places inland. Sporadic from Nova Scotia to Ontario, southward in the United States, and from California to Virginia. Native of Europe. $2n = 22$ (Manton, 1932; Winge, 1925; Ibarra & La Porte, 1947; Mulligan, 1959; van Loon & de Jong, 1978).

Draba verna L. (*Erophila verna* (L.) Chev.)—WHITLOW GRASS, WHITLOW WORT. Annual or winter annual. Fields, lawns, open grassy hillsides and rangeland, waste places, usually where sand predominates. In some places millions of plants are present in a single population. Very common in many areas, sporadic in others, widely distributed in temperate North America. In most localities one of the earliest plants to flower in late winter or early spring. Native of Eurasia. $n = 8$ (Easterly, 1963); $n = 15$ (Mulligan, 1966); $2n = 19 + 1$ (Mulligan, 1966).

***Eruca vesicaria** (L.) Cav. subsp. **sativa** (Miller) Thell.—GARDEN ROCKET. Annual. Waste places and cultivated fields, roadsides, and open rangelands. Sporadic and local in many parts of the United States and Canada; especially abundant and widespread in central and highland southern Mexico. Native of Eurasia. $n = 11$ (Harberd, 1972); $2n = 22$ (Manton, 1932; Wills, 1966).

***Erucastrum gallicum** (Willd.) O. E. Schulz—DOG MUSTARD, ROCKET WEED. Annual or winter annual. Waste places, grain fields, roadsides, orchards, gardens, and railway yards. Common in some areas (e.g., the upper midwestern United States and south-central Canada); sporadic but widespread in other parts of temperate North America. Native of Eurasia. $n = 15$ (Harberd, 1972); $2n = 30$ (Manton, 1932; Mulligan, 1957).

***Erysimum cheiranthoides** L.—WORMSEED MUSTARD. Annual or winter annual. Common in grain fields, pastures, roadsides, sandy creek bottoms, and open hillsides; mainly on disturbed sites or where land is cultivated. Widespread throughout temperate North America including Alaska and the Yukon. Native of Eurasia. $n = 8$ (Jaretsky, 1928; Smith, 1938); $2n = 16$ (Manton, 1932; Mulligan, 1957; Rollins & Rüdenberg, 1977; Harriman, 1978).

Erysimum hieracifolium L.—TALL WORMSEED MUSTARD. Biennial or perennial. Becoming increasingly abundant in pasture land, waste places, and river flats, and on railroad and road embankments. Southern Canada from Nova Scotia to Saskatchewan but most common in eastern Ontario. Local in Wisconsin;

not known from elsewhere in North America. Native of Europe. $2n = 32$ (Tischler, 1934); $2n = 32, 48$ (Polatschek, 1966); $2n = 48$ (Jankun, 1965).

***Erysimum repandum** L.—TREACLE MUSTARD. Annual or winter annual. Roadsides, waste places, gardens, fields, gravel washes, and open rangelands of the cool desert and high plains. Common and widespread in temperate North America. Native of Eurasia. $n = 7$ (Aryavand, 1977); $n = 8$ (Mulligan, 1966); $n = 7, 14$ (Easterly, 1963); $2n = 14, 16$ (Manton, 1932; Polatschek, 1966); $2n = 16$ (Löve & Löve, 1956; Ančev, 1978).

Euclidium syriacum (L.) R. Br. Annual. Roadsides and waste places. Found at widely disparate places in the United States. Native of Eurasia. $2n = 14$ (Jaretsky, 1932).

Hesperis matronalis L.—DAME'S VIOLET. Biennial or perennial. Escaped from cultivation and now widely naturalized. Roadsides, rich moist woodlands, thickets, waste places, and old gardens. Much of temperate North America wherever it has been used as a garden plant. Native of Europe. $n = 8, 16, 24$ (Easterly, 1963); $2n = 24$ (Löve & Löve, 1956); $2n = 24, 28$ (Manton, 1932); $2n = 24, 26, 28$ (Dvořák, 1965).

***Hirschfeldia incana** (L.) Lagrèze-Fossat (*Brassica geniculata* (Desf.) J. Ball). Biennial or perennial. Disturbed moist soils, waste places, along roadsides and canyons, and in a few places in open desert. Oregon, southern Nevada, central and southern California. Native of the Mediterranean region. $n = 7$ (Mayor, 1934).

Hutera cheiranthos (Vill.) Gómez-Campo (*Rhyncosinapis cheiranthos* (Vill.) Dandy). Annual. Roadsides and ballast. Local in New Jersey, North Carolina, and Pennsylvania. Native of southern Europe. $2n = 48$ (Wright, 1936).

Iberis amara L.—WILD CANDYTUFT. Annual or biennial. Escaped from cultivation and only sparingly found in widely disparate localities. Native of Eurasia. $2n = 14$ (Manton, 1932; Bali & Tandon, 1957); $2n = 14, 16$ (Jaretsky, 1932); $2n = 18, 36$ (Bali & Tandon, 1959).

Ionopsidium acaule (Desf.) Reichenb.—DIAMOND FLOWER. Annual. Escaped from cultivation locally in northwestern California and western Oregon. Native of Portugal. $2n = 24$ (Chiarugi, 1928).

***Isatis tinctoria** L.—WOAD, DYER'S WOAD. Winter annual or biennial. Grain fields, orchards, pastures, waste places, and mountainsides. Rapidly spreading into rangelands and mountain pastureland in some areas. Abundant and widespread in western United States; less abundant but common at widely separated places elsewhere in North America. Native of Europe. $2n = 28$ (Jaretsky, 1932; Manton, 1932; Gadella & Kliphuis, 1970).

***Lepidium campestre** (L.) R. Br.—FIELD PEPPERGRASS, COW CRESS, POOR MAN'S PEPPER. Annual. Fields, pastures, meadows, gardens, yards, and waste places; often in grain fields. Widely distributed but sporadic in eastern North America; common and abundant in some areas of western United States and Canada.

Native of Eurasia. $n = 8$ (Easterly, 1963; Hill, 1978); $2n = 16$ (Mulligan, 1957, 1961a; Taylor & Mulligan, 1968).

Lepidium densiflorum Schrader—PEPPERGRASS, GREEN-FLOWERED PEPPERGRASS. Annual. Disturbed habitats, cultivated fields, roadsides, and dry, open soil of plains, prairies, and waste places. Abundant and widespread in the temperate parts of North America including the highland parts of Mexico. Apparently native in some parts of its range in western United States and Canada but said by many authors to be native of Asia and Europe. $n = 16$ (Jaretsky, 1932; Smith, 1938; Rollins, 1966); $2n = 32$ (Manton, 1932; Mulligan, 1957, 1961).

Lepidium heterophyllum (DC.) Bentham. Perennial. Roadsides and disturbed sites. Well-established as a local weed on Vancouver Island, British Columbia, Canada. $2n = 16$ (Manton, 1932; Mulligan, 1961a).

Lepidium latifolium L.—PERENNIAL PEPPERGRASS, BROAD-LEAVED PEPPERGRASS. Perennial. Beaches, tidal shores, wasteland, or somewhat saline irrigated land. Localized in widely separated places in Canada, United States, and Mexico. $2n = 24$ (Manton, 1932; Mulligan, 1957, 1961a; Heiser & Whitaker, 1948; Lessani & Chariat-Panahi, 1979).

Lepidium perfoliatum L.—SHIELD CRESS, CLASPING-LEAVED PEPPERGRASS. Annual. Common along roadsides, on overgrazed lands, edges of fields, grain fields, pastures, and waste ground. Widely distributed in temperate North America, particularly in the western part. Native of Eurasia. $n = 8$ (Jaretsky, 1932; Rollins, 1966); $2n = 16$ (Manton, 1932; Mulligan, 1957, 1961a).

Lepidium ruderale L.—ROADSIDE PEPPERGRASS. Biennial or winter annual. Roadsides, waste places, and old fields. Present in widely separated places, especially in eastern United States and Canada; sporadic elsewhere in North America. Native of Eurasia. $2n = 16$ (Kliphuis, 1977; van Loon & de Jong, 1978); $2n = 32$ (Manton, 1932; Tischler, 1934; Löve & Löve, 1956; Fritsch, 1973).

Lepidium sativum L.—GARDEN CRESS. Annual. Escaped from cultivation. Roadsides, waste places, and cultivated ground. Sporadic in widely separated places, probably in areas where it has been grown as a salad green. Native of Europe. $2n = 16$ (Reese, 1950; Mulligan, 1961a); $2n = 24$ (Vaarama, 1951).

Lobularia maritima (L.) Desv. (*Alyssum maritimum* (L.) Lam.)—SWEET ALYSSUM. Perennial. Escaped from gardens, where it is frequently used as an edging plant. Lawns, cultivated ground, and waste places; sporadic and not always persisting in a given location. Widely naturalized in North America. Native of Eurasia. $2n = 22$ (Borgen, 1969); $2n = 24$ (Larsen, 1955; Manton, 1932; van Loon & de Jong, 1978).

Lunaria rediviva L.—MONEY PLANT. Biennial or perennial. Escaped from cultivation. Waste places, streets, and roadsides; occasional in areas where

it is cultivated as a garden flower. Native of Europe. $n = 14$ (Delay, 1970); $2n = 28+$, 28 + 2B (Manton, 1932); $2n = 30$, 60 (Skalinska *et al.*, 1971).

***Malcolmia africana** (L.) R. Br. Annual. Common and abundant along highways, on disturbed areas, and open rangeland. Intermountain and Great Basin area from Arizona and Nevada northeast to southern Canada. Native to the Mediterranean region. $n = 14$ (Jaretsky, 1928; Bhat, Bakshi, & Kaul, 1974); $2n = 28$ (Manton, 1932).

Malcolmia graeca Boiss. & Spruner. Annual. Pastures and disturbed areas. Escaped from cultivation. Recorded only from Mexico. Native of Europe.

Matthiola bicornis (Sibth. & Sm.) DC.—EVENING STOCK. Annual or biennial. Escaped from gardens. Disturbed waste places; occasional and sporadic. Texas and California. Native of Eurasia.

Matthiola incana (L.) R. Br.—STOCK. Biennial or perennial. Escaped from gardens. Occasional along seacoast bluffs and waste places; usually not persisting in a given locality for long periods. Native of Europe. $n = 7$ (Gardé & Malheiros-Gardé, 1953); $2n = 14$ (Allen, 1924; Corner, 1927; Jaretsky, 1928; Ross & Miller, 1961).

Myagrum perfoliatum L. Annual. Fields and roadsides; uncommon. Apparently escaped from gardens. A few widely separated localities in Canada and the United States. Native of Europe.

Nasturtium officinale R. Br. (*Rorippa nasturtium-aquaticum* (L.) Hayek)—WATERCRESS. Perennial. Escaped from deliberate plantings in streams. In cool water in brooks, rills, springheads, and swamps. Throughout temperate North America, often in remote places in the mountains as well as nearer inhabited areas. Native of Eurasia. $n = 7$ (Easterly, 1963); $n = 16$ (Rodman & Bhargava, 1976; Rahn, 1966; Aryavand, 1977); $2n = 32$ (Jaretsky, 1932; Howard & Manton, 1946; Rollins & Rüdenberg, 1971); $2n = 32$, 48, 64 (Manton, 1932; Tischler, 1934).

Nasturtium microphyllum (Boenn.) Reichenb.—WATERCRESS. Perennial. Escaped from deliberate plantings in streams. In cool water in brooks, springheads, runs, and swamps. Mostly in eastern Canada and eastern to southeastern United States; sporadic elsewhere in temperate to cool areas. Native of Eurasia. $2n = 64$ (Mulligan, 1964).

***Neslia paniculata** (L.) Desv.—BALL MUSTARD. Annual. Often abundant; grain fields, waysides, waste places, and cultivated land. Nearly throughout Canada to Alaska, and from the northern plains to the eastern United States; sporadic elsewhere. Native of Eurasia. $n = 7$ (Jaretsky, 1928); $2n = 14$ (Manton, 1932; Mulligan, 1957; Taylor & Mulligan, 1968).

***Raphanus raphanistrum** L.—JOINTED CHARLOCK, WILD RADISH. Annual or winter annual. Cultivated fields, disturbed waste places, roadsides, orchards, and hillslopes. Widely distributed, especially in eastern North America and southward at high elevations; very abundant in parts of Mexico and Central

America. Native of Eurasia. $n = 9$ (Shive, 1969; Harberd, 1972); $2n = 18$ (Tischler, 1934; Rohweder, 1937; Löve & Löve, 1956; Mulligan, 1961b).

***Raphanus sativus** L.—RADISH, WILD RADISH. Annual. Common and abundant in grain fields, gardens, orchards, coffee plantations, and cultivated land generally; roadsides and waste places. Probably introduced from Eurasia as a seed contaminant as well as an escape from gardens. Widespread in temperate and cool parts of North America, including the highland areas of Mexico and Central America. Native of Eurasia. $n = 9$ (Harberd, 1972; Sato, 1955); $2n = 18$ (Manton, 1932; Morris & Richharia, 1937; Heiser & Whitaker, 1948; Sato, 1955).

Rapistrum rugosum (L.) All. Annual. Roadsides and waste places of cities and towns. Infrequently encountered at widely separated sites in Canada, Mexico, and the United States. Native of the Mediterranean region. $2n = 16$ (Manton, 1932).

Rapistrum perenne (L.) All. Perennial. Waste places. Apparently established in a limited area of southeastern Saskatchewan, Canada. Native of Europe.

Rorippa amphibia (L.) Besser. Perennial. Quiet waters and shores or moist, disturbed areas. Sporadic in eastern North America. Native of Eurasia. $2n = 16$ (Howard, 1947); $2n = 32$ (Wulff, 1939).

***Rorippa austriaca** (Crantz) Besser—AUSTRIAN FIELD CRESS. Perennial. Pastures, cropland, and waste areas, usually where moisture is plentiful. Widely scattered localities in Canada and the United States. Native of Europe. $2n = 16$ (Manton, 1932; Howard, 1947).

Rorippa indica (L.) Hiern var. **apetala** (DC.) Hochr. Annual or biennial. Waste ground and gardens. Limited to a few localities at widely separated places in the United States and Central America. Native of Southeast Asia.

***Rorippa sylvestris** (L.) Besser—YELLOW CRESS, CREEPING YELLOW CRESS. Perennial. Gardens, around ponds, along ditches and disturbed stream banks, in moist meadows, fields, and nurseries. Common in northeastern United States and adjacent Canada; sporadic elsewhere in North America. Native of Europe. $n = 16$ (Easterly, 1963; Naqschi & Javeid, 1976); $2n = 32$ (Manton, 1932); $2n = 32, 40, 48$ (Jonsell, 1964); $2n = 48$ (Howard, 1946, 1953; Löve & Löve, 1956; Gadella & Kliphuis, 1967; Rollins & Rüdenberg, 1977).

***Sinapis alba** L. (*Brassica hirta* Moench). Annual. Escaped from cultivation, fields, roadsides, and waste places; abundant in some localities. Widespread but sporadic in North America, including highland areas of Mexico and Central America. Native of Eurasia. $2n = 24$ (Yarnell, 1956).

***Sinapis arvensis** L. (*Brassica kaber* (L.) L. C. Wheeler)—WILD MUSTARD, CHARLOCK. Annual. Grain and flax fields, gardens, cultivated land generally, waste places, especially newly disturbed places including roadsides; common and abundant. Well known as a seed contaminant. Nearly throughout the temperate agricultural areas of North America, including the highlands of

Mexico and Central America. Native of Europe. $n = 9$ (Shive, 1969); $n = 8, 16$ (Easterly, 1963); $2n = 18$ (Yarnell, 1956).

***Sisymbrium altissimum** L.—TUMBLE MUSTARD, JIM HILL MUSTARD. Annual or winter annual. Fields, roadsides, waste places, railroad yards and rights-of-way, disturbed areas of prairies and high deserts; common and abundant. Throughout the temperate and arid parts of central and northern North America; sporadic southward in Mexico and beyond. Native of Eurasia. $n = 7$ (Easterly, 1963; Rollins, 1966; Rollins & Rüdenberg, 1977); $2n = 14$ (Manton, 1932; Smith, 1938; Mulligan, 1961b; Ančev, 1978).

***Sisymbrium irio** L.—LONDON ROCKET. Annual. Fields, orchards, roadsides, waste places, and open deserts. Often abundant in southwestern United States and Mexico; sporadic elsewhere, particularly northward. Native of Europe. $n = 7$ (Rollins & Rüdenberg, 1977; Aryavand, 1977); $n = 14$ (Amin, 1973); $2n = 14$ (Jaretsky, 1932); $2n = 14, 28, 42, 56$ (Khoshoo, 1955, 1957).

***Sisymbrium loeselii** L.—TALL HEDGE MUSTARD. Annual. Field margins, grain and fallow fields, roadsides, and waste places. Common and abundant in some areas of the plains region of Canada and the United States; sporadic elsewhere in widely separated localities of North America. Native of Eurasia. $2n = 14$ (Jaretsky, 1932; Mulligan, 1957).

***Sisymbrium officinale** (L.) Scop.—HEDGE MUSTARD. Annual. Roadsides, edges of fields, farmyards, gardens, and waste places; usually on disturbed sites, sometimes on open grazing land (especially in parts of Mexico); common and abundant in some areas. Most of temperate North America, but sporadic southward to Central America. Native of Europe. $n = 7$ (Easterly, 1963; Rollins & Rüdenberg, 1977); $2n = 14$ (Wulff, 1937; Rohweder, 1937; Heiser & Whitaker, 1948; Ančev, 1978; Taylor & Mulligan, 1968).

***Sisymbrium orientale** L. Annual. Street margins, roadsides, and waste places generally, but also invading disturbed, open desert areas. Nevada to central and southern California; sporadic elsewhere in southwestern United States and adjacent Mexico. Native of Mediterranean region. $n = 7$ (Rollins, 1966); $2n = 14$ (Jaretsky, 1932; Diers, 1961; Ančev, 1978).

Sisymbrium polyceratium L. Annual. Roadsides and waste places; uncommon. Widely separated localities in the United States. Native of Eurasia.

Teesdalia nudicaulis (L.) R. Br. Annual or winter annual. Infrequent in sandy fields, lawns, roadsides, and other disturbed habitats. States of the eastern seaboard and in western Oregon, Washington, and British Columbia. Native of southern Europe and north Africa. $n = 18$ (Böcher & Larsen, 1958); $2n = 36$ (Manton, 1932; Jaretsky, 1932; Tischler, 1934; Rohweder, 1937; Gadella & Kliphuis, 1966).

***Thlaspi arvense** L.—STINKWEED, FRENCHWEED, FIELD PENNY CRESS. Annual or winter annual. Grain and hay fields, gardens, roadsides, and waste places; grazing land in some places and in some areas ascending lower reaches of mountains; common and abundant. Nearly throughout temperate North

America but seeming to avoid the hotter and more humid areas of Mexico and Central America. Native of Europe. $n = 7$ (Wiens & Halleck, 1962; Easterly, 1963; Pinkava *et al.*, 1974); $2n = 14$ (Manton, 1932; Löve & Löve, 1954; Mulligan, 1957; Ančev, 1976).

Thlaspi perfoliatum L.—PENNY CRESS. Annual. Roadsides, fields, and waste places; uncommon but sometimes locally abundant. Mostly in central and eastern United States and adjacent Canada; sporadic elsewhere in North America. Native of Europe. $2n = 42$ (Jaretsky, 1932; Ančev, 1978); $2n = 70$ (Jaretsky, 1932).

NATIVE TAXA OF THE CRUCIFERAE THAT HAVE BECOME WEEDY

Most of the native cruciferous weeds do not have common names. In some books common names have been coined for these plants, but they are not common names in the sense that they are generally used by nonprofessional botanists, horticulturists, or agronomists.

Arabis glabra (L.) Bernh. (*Turritis glabra* L.)—TOWER MUSTARD. Biennial. Roadsides, banks, open woods, fields, lake and stream margins, cliffs and rocky places, often on disturbed sites; in the mountains as well as at lower elevations; common and often abundant. Eastern United States and Canada to California, north to British Columbia; less common or absent in the plains region. According to some authors (e.g., Rydberg, 1917, 1923), this species is a native of Europe and is wholly naturalized in North America. However, this seems not to be the case. *Arabis glabra*, although weedy in many places, is truly at home as part of the natural vegetation at a very large number of stations. It is probable that both native and Old World populations have contributed to the weedy populations now present in North America. The fact that there is an undoubtedly native taxon (*A. glabra* var. *furcatipilis* Hopkins, found in Utah and California) supports the conclusion that *A. glabra* var. *glabra* is indigenous to North America, as well as to Europe and Asia. $n = 16$ (Taylor & Mulligan, 1968; Rodman & Bhargava, 1976); $2n = 12$ (Titz, 1967); $2n = 16, 32$ (Hara, 1952).

Athysanus pusillus (Hooker) Greene. Annual. Inconspicuous but abundant in overgrazed pastureland, orchards, hillsides, and disturbed places; usually avoids truly cultivated land. Common in the inner Coast Ranges of California; from Idaho to British Columbia and southern California. Native of western United States and Canada.

Cakile edentula (Bigelow) Hooker—SEA ROCKET. Annual. Strand plants introduced from the east coast of North America to the shores of the Great Lakes and to the sandy beaches of the Pacific Ocean along the west coast; also in Australia, New Zealand, and the Azores. Gradually being displaced in some areas by *Cakile maritima*. Native of the east coast of North America from Labrador to Virginia. $2n = 18$ (Kruckeberg, 1948; Mulligan, 1964; Taylor & Mulligan, 1968).

Cardamine parviflora L. var. **arenicola** (Britton) O. E. Schulz. Annual. Shady brooks and woods, pastures, wet meadows, roadsides, and fallow fields, spreading locally to fields and roadsides. Quebec to Florida and northwestward from Louisiana and Texas to British Columbia; least common and sporadic west of Minnesota (the populations found may be introductions from its more easterly range, where it is often abundant).

Caulanthus lasiophyllus (Hooker & Arnott) Payson (*Microsisymbrium lasiophyllum* (Hooker & Arnott) O. E. Schulz). Annual. Abundant in open desert (usually in shade of bushes), pastures, roadsides, wasteland, and other disturbed places. Utah to Arizona, west to Baja California, and north to southwestern Washington; probably introduced northward from California, where it is very common in the central and coastal valleys. $n = 14$ (Rollins, 1966; Rollins & Rüdenberg, 1979).

Descurainia impatiens (Cham. & Schlecht.) O. E. Schulz. Annual. Disturbed places and cultivated lands; often abundant. Central and southern Mexico. Native of Mexico.

Descurainia pinnata (Walter) Britton—TANSY MUSTARD. Annual. Roadsides, fallow fields, dry sandy soils on hillsides, prairie, desert plains, open woodland, and waste places; abundant and common. Its several subspecies and varieties are widely distributed in Canada and the United States; less common southward in Mexico and beyond. Native of North America. Present range undoubtedly much wider than its original distribution. $n = 7$ (Rollins & Rüdenberg, 1977).

Descurainia richardsonii (Sweet) O. E. Schulz—GRAY TANSY MUSTARD. Annual. Calcareous gravels, open sandy woodlands, prairies, plains, fields, and waste places; abundant and common. The species, including its subspecies and varieties, most frequently found in central and western North America from Alaska to Mexico; sporadic elsewhere. Native of North America. $n = 7$ (Rodman, 1978); $2n = 14$ (Mulligan, 1961b); $2n = 14, 28, 42$ (Baldwin & Campbell, 1940).

Descurainia virletii (Fourn.) O. E. Schulz. Annual. Disturbed places and cultivated areas; abundant and common. Central highlands of Mexico. Native of Mexico. $n = 14$ (Rollins & Rüdenberg, 1977).

Draba brachycarpa Nutt. Annual or winter annual. Lawns, roadsides, pastures, fallow fields, and disturbed places. Abundant and common in central and southern United States; adventive and sporadic in areas outside of its natural range. Native of south-central United States. $n = 8$ (Smith, 1969); $2n = 24$ (Rollins & Rüdenberg, 1971).

Draba cuneifolia Nutt. Annual or winter annual. Prairie pastures, lawns, fallow fields, sandy disturbed soils, and waste places; abundant and common. Southern and southwestern United States and adjacent Mexico. Native of southwestern North America. $n = 16$ (Rollins & Rüdenberg, 1971).

Draba nemorosa L. Annual or winter annual. Open woods, pastures, lawns, fallow fields, roadsides, and disturbed places; abundant and common in some

areas. Central and northern North America; sporadic and often adventive elsewhere, particularly eastern United States and Canada. Native of North America.

Draba reptans (Lam.) Fern. Annual. Open sandy areas, roadsides, pastures, and disturbed places; common in some parts of its range where it has become weedy, sporadic in other parts. Eastern and central United States and westward to Washington, Oregon, and northern California. Native of North America.

Erysimum inconspicuum (S. Watson) MacM. Perennial. Roadsides, field-margins, disturbed areas generally. Widely distributed in central, west-central, and northern North America; adventive eastward and southward. Native of present range, but its geographic distribution is much wider now than before the advent of agriculture in the region of its occurrence. $n = 27$, $2n = 54$, 162 (Mulligan, 1966).

Leavenworthia uniflora (Michaux) Britton. Annual. Fields and roadsides, usually in cedar glade areas; exceedingly abundant. Kentucky and Ohio to Alabama and Missouri. Although native to most of its present range, the plants have moved from their original habitats. $n = 15$ (Rollins, 1963); $2n = 30$ (Baldwin, 1945). Other species (*L. alabamica* Rollins, *L. crassa* Rollins, *L. exigua* Rollins, *L. stylosa* A. Gray, and *L. torulosa* A. Gray) are in fields and pastures as well as cedar glades. Cornfields in low places where moisture persists in the spring are often completely covered with *Leavenworthia* plants. These manage to produce viable seed before tilling is possible, thus assuring a new population each year.

Lepidium. Most of the native annual species of *Lepidium* become weedy under certain circumstances, and some species, such as *L. lasiocarpum* Nutt. and *L. ramosissimum* A. Nelson, are weedy nearly throughout their ranges. With these, it is now impossible to determine their exact indigenous boundaries because of the ease with which they move from one area to another. The most common and widely distributed native annual is *L. virginicum* L.

Lepidium virginicum L.—POOR MAN'S PEPPERGRASS, PEPPERGRASS, VIRGINIA PEPPERGRASS. Annual or winter annual. Fields, meadows, pastures, open rangeland, roadsides, and waste places; particularly on disturbed sites. Common and widespread nearly throughout North America. There are a number of recognized infraspecific taxa. Although a native of North America, *L. virginicum* has been widely introduced to other continents. $n = 8$, 16 (Easterly, 1963); $2n = 32$ (Smith, 1938; Mulligan, 1961a; Rollins & Rüdenberg, 1971).

Lesquerella. The annual species are often abundant where they occur, and some of these definitely have weedy tendencies. The most notable are: 1) *Lesquerella densipila* Rollins. This species often occupies entire fields in central Tennessee and is along roadsides in northern Alabama; it has apparently spread from Tennessee to Alabama. 2) *Lesquerella gracilis* (Hooker) S. Watson. Grain fields, railroad rights-of-way, and sandy roadsides. Native in central and east-central Texas; adventive in Illinois, Missouri, Mississippi, and Tennessee. 3) *Lesquerella gordonii* (A. Gray) S. Watson. Abundant in open

disturbed areas and along roadsides. Kansas, Oklahoma, and Texas west to western Arizona. 4) *Lesquerella lasiocarpa* (Hooker) S. Watson. Open disturbed areas and along roadsides. Southwestern Texas and adjacent Mexico. 5) *Lesquerella lescurii* (A. Gray) S. Watson. Old fields, river bottoms, and roadsides. Central Tennessee.

Rorippa. The native annual species show weedy tendencies, and at least one perennial, *R. sinuata* (Nutt.) A. S. Hitchc., is a roadside and field weed in some places, usually in sandy soils. So far it is not known to be noxious even though the plants spread by underground rhizomes. Moist places, such as the banks of streams or irrigation ditches, are favorite habitats. *Rorippa curvipes* Greene, an annual that is abundant in the Rocky Mountain region of the western United States, occurs sporadically eastward as a weed, with at least one locality in Michigan. $2n = 16$ (Rollins, 1961). *Rorippa palustris* (L.) Besser is a widespread annual. As a weed it occurs in open disturbed areas, along roadsides, on field-margins, and in waste places, usually in moist to wet soils. $2n = 32$ (Jørgensen, Sørensen, & Westergaard, 1958; Mulligan, 1964). *Rorippa palustris* var. *palustris* is native to Europe and perhaps also to some areas of eastern United States and Canada. As a weed it is also introduced outside its native range, either from Europe or from native populations. Populations of most of the subspecies and varieties of *R. palustris* occur as weeds nearly throughout the United States and the southern half of Canada; many of these are outside the presumed natural geographic range of the species. $2n = 32$ (Löve & Löve, 1975). Other annual species, such as *R. sessiliflora* (Nutt.) A. S. Hitchc., $2n = 16$ (Jonsell, 1968), and *R. teres* (Michaux) Stuckey, which are found primarily in the central and southern United States, also have weedy tendencies. They often occupy open disturbed sites, roadsides, pastures, and cultivated land. Although the degree to which they have moved outside of their original geographic pattern of occurrence is difficult to determine, it is almost certain that many weedy populations now in existence have come into being since man disturbed the original vegetational cover.

Sibara virginica (L.) Rollins. Annual. Abundant in old fields, clearings, roadsides, pastures, and other open areas. Distributed from the Atlantic coast to central Texas, and then disjunct to southern California. In the vegetative state this species is often confused with *Cardamine hirsuta* L. The two grow together in many places. $n = 8$ (Rollins & Rüdenberg, 1977); $2n = 16$ (Rollins, 1966).

Streptanthella longirostris (S. Watson) Rydb. Annual. Abundant along sandy roadsides and on disturbed sites elsewhere, also in open desert. Southwestern Wyoming to New Mexico, westward to California and Baja California. It is doubtful whether this species exceeds its native range, but its great abundance in disturbed sites definitely shows its weedy tendencies.

Tropidocarpum gracile Hooker—DOBIE POD. Annual. Grassy slopes, open swales, field-margins, roadside slopes, open chapparal, and open desert. This species has weedy tendencies but seems to avoid cultivated fields. The plants

are often so dense that they form a tangled mass. Very abundant in the southern inner Coast Ranges of California, where it is sometimes the dominant herb; also in southern California and northward from the Central Valley. Native of California. $n = 8$ (Rollins, 1966; Rollins & Rüdenberg, 1979).

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Because of continually increasing production costs, the Editorial Committee of the *Journal of the Arnold Arboretum* is requesting authors to help defray publication expenses. Beginning with manuscripts received and accepted for publication as of March, 1980, a page charge will be levied. Acceptance of manuscripts for the Journal will, however, continue to be based solely on appropriateness and scientific merit, not on an author's ability to meet page costs. Information on page charges and general editorial policies can be obtained from the Managing Editor.

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